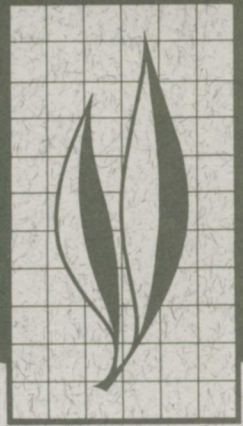


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Bioecological and Population Studies of the
Cottony-cushion Scale, *Icerya purchasi* Mask.,
and Its Natural Enemies, *Rodolia cardinalis*
Mul. and *Cryptochaetum iceryae* Will., in
Southern California

José R. Quezada and Paul DeBach

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Competitive interactions between the two natural enemies of *Icerya purchasi*—*Rodolia cardinalis* and *Cryptochaetum iceryae*—were studied in detail in order to throw more light on the question of the introduction of multiple natural enemies as a biological control policy. The host, a major citrus pest accidentally introduced in 1868 from Australia, has been under control since 1888–1889, when its highly specific natural enemies (also from Australia) were imported for that purpose. Three different climatic regions of southern California were the study sites: the desert, the coast, and the interior. Life table studies of the scale indicated that it is maintained under control at very low population levels in the desert by vedalia and on the coast by *Cryptochaetum*, with competition causing displacement in both areas. In the interior, the two enemies seasonally share their prey in different proportions and are fairly even in their competitive abilities—vedalia usually taking more prey during the summer and fall, the fly taking more during the winter and early spring. In the interior, three generations of the host occurred in a year, while those of vedalia and *Cryptochaetum* averaged 12 and 8, respectively. Some host plants restricted vedalia development, and certain species of ants interfered with *Cryptochaetum*. Competition results in microhabitats also varied, depending on prevailing environmental conditions and the time at which an enemy finds a scale colony. The “coexistence” of vedalia and *Cryptochaetum* in the interior is thought to be only apparent and maintained by the dispersal of *Cryptochaetum* from their coastal area of dominance. Coexistence experiments in the interior showed displacement of the fly by vedalia to occur after nine generations. Competition between the two natural enemies did not increase host survival. These extensive studies provided strong support for the policy of importation of multiple natural enemies.

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INTRODUCTION

CONTROL OF THE COTTONY-CUSHION SCALE, *Icerya purchasi* Maskell, by its natural enemy, the vedalia beetle, *Rodolia cardinalis* (Mulsant), in California was the first outstanding and now classical example of biological control (fig. 1). *Icerya purchasi*, accidentally introduced in 1868 from Australia (Doutt, 1964), became so abundant in the absence of its natural checks that in a few years it threatened the whole citrus industry of California. The introduction of the predatory vedalia beetle from Australia in 1888–1889 brought about the rapid control of the pest in southern California. At about the same time, or perhaps even a little earlier (Smith and Compere, 1916), a parasitic fly, *Cryptochaetum iceryae* (Williston), was also introduced and colonized in San Mateo and Los Angeles counties. The value of the fly, however, was over-shadowed by the outstanding success of vedalia on commercial citrus in the south. Thus, nearly all the credit for the control of the scale has been given to the beetle, although Riley

(1889) emphasized the potential of *Cryptochaetum* and expressed his hope for the success of the parasite. A few other workers have suggested that the fly may be equally effective, or even superior, to the vedalia beetle in the control of the cottony-cushion scale in certain areas of the scale's distribution (Smith and Compere, 1916; Essig, 1958; Thorpe, 1930; Clausen, 1956; Bartlett and Lagace, 1960).

Icerya purchasi has a wide range of distribution throughout the state and can be found in the mild coastal areas, the interior regions, and in the hot, dry, desert areas. It is found not only on citrus but on a large number of alternate host plants as well, some of which provide good protection to and are important in the survival of the pest.

The cottony-cushion scale is usually maintained at low population levels by either or both of its natural enemies on all of the host plants and in all places where it occurs in California. Climate, however, directly or indirectly influences the distribution and abundance

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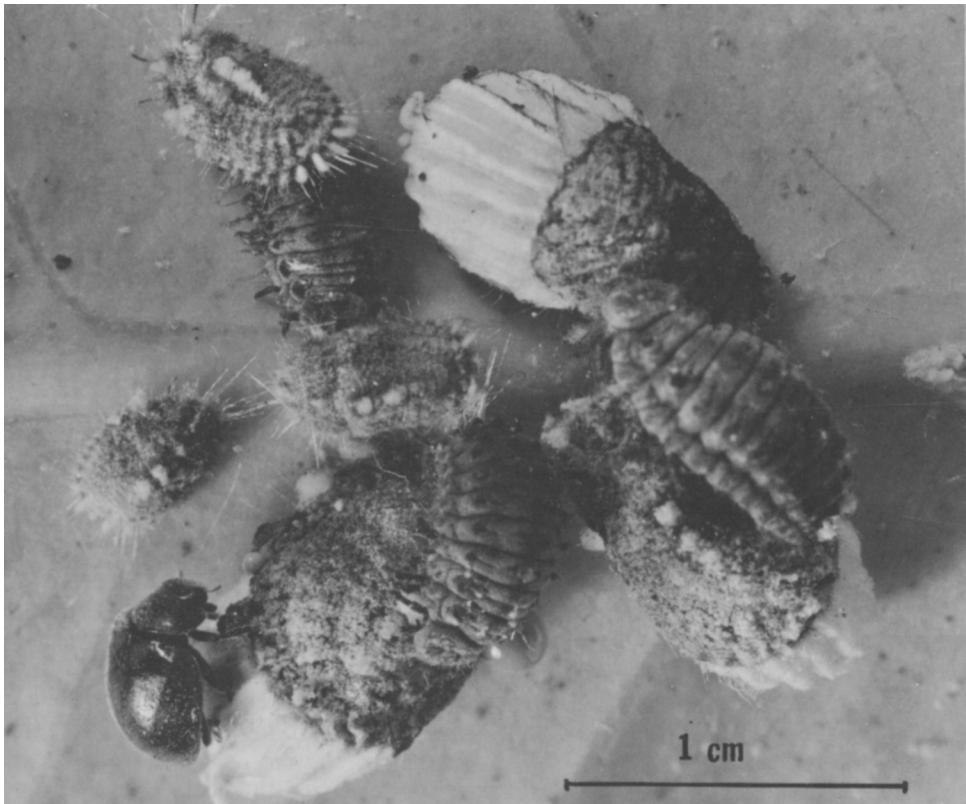


Fig. 1. Adult and larvae of vedalia attacking *Icerya purchasi*.

of both enemies of the scale. *Cryptochaetum* is dominant in coastal regions, while vedalia is dominant in the desert areas. In the interior, both species overlap and share their prey in different proportions throughout the year. Competitive advantage between the two is rather evenly balanced in this region, and in spite of a variable seasonal dominance of either species over the other, both are common throughout the year. Occasional upsets of the scale's population balance may occur in all districts on individual plants or in small areas. These can be ascribed to the adverse effect of various factors on natural enemies, such as ants and insecticides.

Both vedalia and *Cryptochaetum* have been found to be highly specific in relation to the host scale and will not

feed or reproduce on any other host in California. From this point of view, the two species can be said to be ecological homologues as defined by DeBach and Sundby (1963). The ecological niches of both natural enemies are not identical in the strictest sense. Vedalia preys on all stages of the scale, while *Cryptochaetum* parasitizes the host from the second stage onward. However, as these authors suggest: "If one essential component of the niches of two species is identical (such as identical food), then the two species are ecological homologues to this extent." They are considered true ecological homologues for all practical purposes in this study.

Our examination of the competitive interactions between *Rodolia cardinalis* and *Cryptochaetum* has thrown some

light on a controversial basic ecological question. Turnbull and Chant (1961) have questioned the value of multiple introductions of natural enemies and suggested that two or more biotic agents attacking a single host species may interfere with each other to the advantage of host survival. According to this hypothesis, *Icerya purchasi* populations in California, for example, may be enhanced rather than suppressed as a result of competition between its two natural enemies.

The studies reported here were undertaken to explore this hypothesis and the mechanisms of competition between the

vedalia beetle and the parasitic fly, as well as their relative and absolute efficiency in population regulation of the scale.

Three different climatic regions of southern California were selected for the studies: the desert (Palm Springs), the interior (Riverside), and the coast (Rancho Santa Fe). It was necessary to find out if the general average densities attained by the scale in the three different regions were different, and if the control exerted by its natural enemies was hindered in any way as a result of their competition, in order to evaluate the assumptions of Turnbull and Chant.

MATERIALS AND METHODS

All laboratory tests were conducted under insectary conditions where the temperature was maintained at $80 \pm 2^\circ$ F, and the relative humidity at 55 ± 5 per cent, unless otherwise stated. Undisturbed citrus orchards—that is, orchards that had not been sprayed for several years—were secured in each of the three regions of southern California to make field observations under natural conditions. For the interior, the Biological Control Grove at the University of California, Riverside, was used. An undisturbed Valencia orange orchard was secured in Rancho Santa Fe near the coast. In the desert (Palm Springs), only a small, untreated, backyard orchard could be obtained.

Rearing methods

Icerya purchasi. In order to have a good supply of scale colonies available for different aspects of the work, a routine rearing method was used. Reproducing scales were obtained in the field and their crawlers allowed to settle on different host plants as was convenient. The plants were potted in 1-, 3-, and 5-gallon containers according to size and were maintained in a greenhouse at a

temperature of $80 \pm 2^\circ$ and 65 ± 5 per cent relative humidity. By allowing the crawlers to settle at different times, different scale stages were available as needed. Plants infested were principally *Citrus* spp., *Pittosporum tobira*, *Cocculus laurifolius*, *Acer oblongum*, *Spartium junceum*, *Cassia artemisoides*, and *Nandina domestica*. Of all these hosts, *P. tobira* proved to be the ideal one for rearing purposes, supporting colonies of scales for longer times than other plants without deterioration.

Rodolia cardinalis. The vedalia beetle was reared by placing one or two pairs in a $2 \times 2 \times 2$ ft sleeve cage whose bottom fit a pot containing a citrus or *Pittosporum tobira* plant infested with scales. The beetles were also reared, when closer observations were needed, in one-pint carton containers covered with a petri dish bottom. Scale-infested leaves from the same plants were regularly provided for the beetles and their growing larvae.

Cryptochaetum iceryae. The fly parasite, as pointed out by Thorpe (1930), needs a greater space than does the vedalia beetle for rearing and normal behavior; thus a $7 \times 4 \times 4$ ft cage was used to secure normal oviposition. Cit-

rus and *Pittosporum tobira* plants infested with second- and third-stage scales were offered, since these stages are most suitable for the parasites.

Competition cages

Four $7 \times 4 \times 4$ ft cages were necessary in order to run competition tests and allow the observer to work inside with ease. The top and sides of the cages were covered with plastic screen (50 mesh per sq cm), while the bottom was anchored to the ground. A 5×2 ft screened door permitted entrance to each cage and movement of plant material in and out. Scale-infested plants were placed on a bench inside each cage. *Cryptochaetum* and vedalia were released in different sequences and observations on their behavior recorded, as well as data on the outcome of their competitive interactions. One cage was also used for observations on the coexistence of both species.

Infestation of alternate host plants in the field

Controversial reports occur in the literature regarding certain effects of some host plants on the natural enemies of *I. purchasi* (Bodenheimer, 1951; Priore, 1963). For the tests reported here, therefore, some of the host plants involved in those reports, as well as other host plants were infested, and their effects on the scale's acceptability by its enemies were evaluated. One hundred scale crawlers were transferred to small paper containers (5 cc) with a camel's hair brush from the producing adults. The containers were attached with masking tape to a branch or twig of the selected plant. The paper container provided an initial shelter for the crawlers, from which they slowly moved out and began to settle nearby. Up to 42 per cent settling of crawlers was obtained with this method. Plants infested in the field were: *Cocculus laurifolius*,

Spartium junceum, *Acer oblongum*, *Ricinus communis*, *Punica granatum*, *C. artemisoides*, *C. cyclops*, *Cassia* spp., *Citrus* spp., *Pittosporum tobira*, and *Nandina domestica*. These plants were located at the University of California, Riverside campus, as well as in parks and backyards in Riverside, San Bernardino, Colton, Loma Linda, and Redlands. They were periodically observed; and when the scale colonies were large enough, samples were taken to observe and record any development of natural enemies.

Collecting scale material in the field

Samples of naturally occurring and artificially induced infestations of *I. purchasi* were taken from different host plants, during different periods, and different areas of southern California, especially from Los Angeles, Orange, Riverside, San Bernardino, and San Diego counties. Samples from Ventura and Santa Barbara counties, the Central Valley, and the San Francisco Bay Area were also secured through the help of various persons. When convenient, pruning shears were used to take sequential samples from the same plant as frequently as possible. The samples, placed in paper bags and brought to the laboratory, were confined in rearing cages to await emergence of the natural enemies. For every sample, all pertinent data was recorded on a specially printed card.

Assessing mortality factors of the scale

Data were obtained to develop life tables of the cottony-cushion scale to ascertain the causes of scale mortality at different stages, as well as their survival and fecundity. Life table studies were carried out in each of the three regions. Scales were located on citrus tree leaves or twigs and individually



Fig. 2. Tagged individual *I. purchasi* used in life table studies. Scale molts remain along leaf vein, and the adult with its egg sac is seen on top.

tagged, a number being assigned for each scale. One hundred scales were tagged in each orchard and during different seasons. Scales were inspected every other day in Riverside and at least once a week in the other two regions. Data were recorded on mimeographed forms. Observation of the scales was facilitated by the short distance a scale moves before settling again when it molts. It is common to find an adult scale attached to the underside of a leaf not far from all of its exuviae on the same leaf (fig. 2). Colonies of the scale were also tagged in the

U.C. Biological Control Grove at Riverside. The locations of individual scales were mapped in a sketch of the branch or twig. The fate of the colony was in this way followed with considerable accuracy. Data recorded in life table studies included: molts, mortality due to *vedalia*, mortality due to *Cryptochaetum*, mortality due to unknown causes, scales that reached maturity and produced crawlers, and scales that were lost. Life table studies also provided valuable data on the life cycles and habits of the scale and its natural enemies. Most of the field data related to the biology of the natural enemies, reported in appropriate sections, were obtained while carrying out the life table studies of the scale.

Using ants as a check method

To test the effects of ant interference with the activities of the natural enemies, a comparison was made between trees in a young lemon orchard in Rancho California, on which ants were excluded by using tanglefoot around the trunks with a group of trees on which ants were allowed to remain active.

Using sleeve cages as a check method

Sleeve cages described by Smith and DeBach (1942) and DeBach, Dietrick, and Fleschner (1949) were used in a Valencia orange plot at Rancho Santa Fe, where *Cryptochaetum* was strongly dominant over *vedalia*. This test was conducted to determine whether the fly alone was capable of controlling the cottony-cushion scale at low population densities.

BIOECOLOGICAL STUDIES

Biology of *Icerya purchasi*

This scale has been the subject of extensive studies in California (Riley, 1887, 1889; Coquillett, 1888; Quayle,

1938), in other places in the United States (Gossard, 1901; Macgillivray, 1921; Hughes-Schrader, 1930), and many countries around the world (Ku-

wana, 1922; Vayssiere, 1926; Bodenheimer, 1930, 1933, 1934, 1951; Leonard, 1932; Fonseca and Autuori, 1938; Chang and Huang, 1963).

Life cycle. Hughes-Schrader (1930) established that the so-called females of *I. purchasi* are hermaphrodites capable of self-fertilization. The length of the life cycle of the scale in southern California (where Riverside is located) varies according to the time of the year.

The egg sacs (fig. 3E) contain between 325 and 450 eggs. The eggs are elongate, oval, pink and smooth. Observations carried out in the summer of 1968 showed that an average of 76 per cent crawlers hatched from ten groups of 100 eggs. The 23.3 per cent mortality was remarkably close to the 20 per cent obtained by Kuwana (1922) in Japan. After an incubation period that varies according to the season, the crawlers hatch (fig. 3A). They are reddish, and their legs and antennae are black. During the first three or four days, the crawlers remain near the mother scale, under the egg sac, or on top of it. Their size never exceeds 0.5 mm in length. Then they start moving and finally settle along the leaf veins, or on branches, in the immediate area. They become covered with white wax plates (fig. 3B) shortly after settling. Tests conducted during the summer of 1968 indicated that, even under the optimal conditions (i.e., protected habitats), only about half of the crawlers were able to settle on their host plants and attain further development. Only 12 per cent of the crawlers would settle on citrus plants in the field. Crawler-settling may vary according to the season of the year, and probably will be different on different host plants as well. The first instar nymph lasts from two to three weeks, after which it molts. The second instar nymph (fig. 3C) is about 1.5 mm long, reddish-brown with orange on the ventral side. The legs and an-

tennae are black. This nymph moves a small distance from its cast skin, and becomes fixed to start feeding again. It soon becomes covered with wax plates. This instar lasts from two to three weeks.

The third instar nymph (fig. 3D) is also reddish-brown, about 4 mm long. The hairs on its integument, which are very small in previous stages, become larger, darker and stout, and grouped in tufts. This instar lasts between two and three weeks, then it molts, and becomes the adult stage. The adult is oval and convex. It soon becomes covered with wax, which projects from the sides of the body as long filaments. The egg sac begins to appear as a posterior narrow white fringe after about three weeks and gradually enlarges, sometimes attaining as much as six times the length of the scale body. The egg sac (fig. 3E) shows the characteristic longitudinal grooves in the species. The adult stage, from its beginning to the production of eggs, lasts between four to six weeks, with occasional prolongations to eight weeks in the winter. The duration of the life stages of the scale in Riverside are presented in table 1.

The life cycle of the scale in Riverside ranges from a minimum of 96 days in the summer to 144 days in the winter.

Once they become fixed to the host plant and begin feeding, all instars of *I. purchasi* produce honeydew—the older ones more copiously. The honeydew attracts several types of insects, such as ants, flies, and bees, and has considerable nutritive value with several sugars and amino acids (Ewart and Metcalf, 1956).

Male scale production. Hughes-Schrader (1930) demonstrated the hermaphroditic condition of *I. purchasi* and gave an account of the mating habits of the scale. The scales are capable of self-fertilization, the resulting diploid individuals being hermaphro-

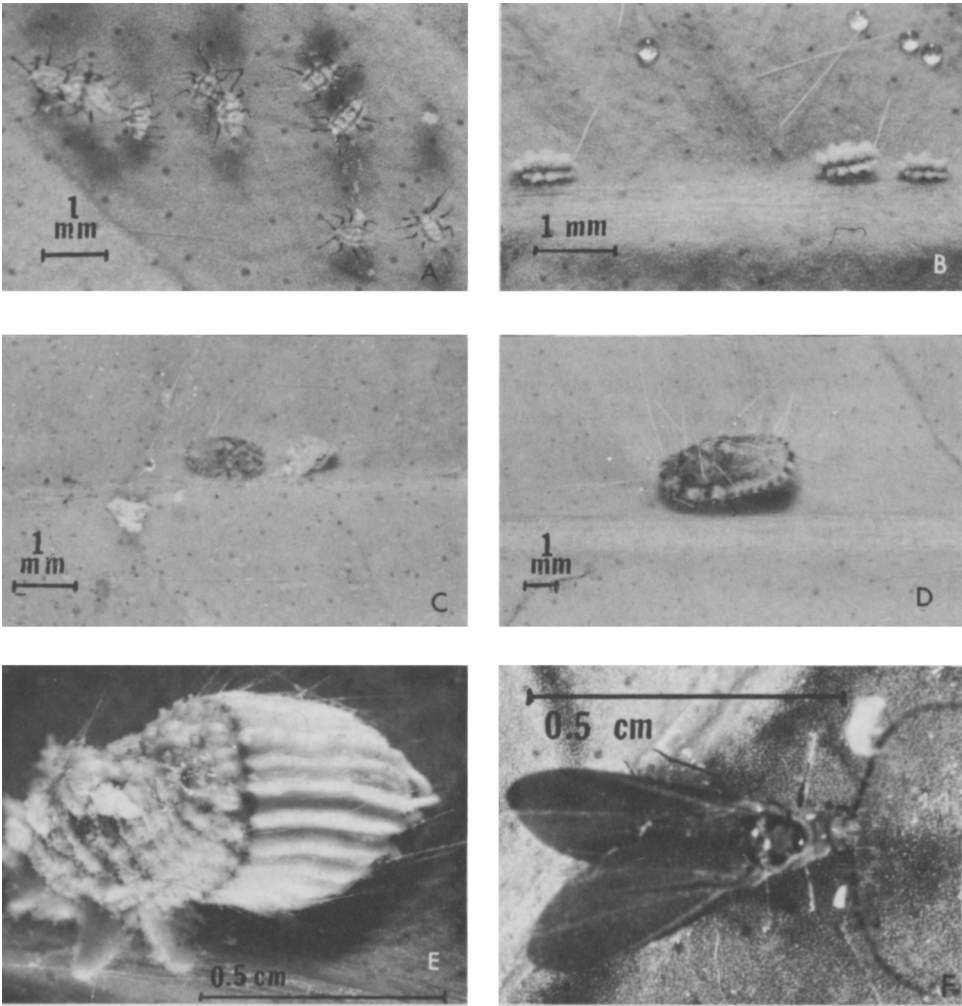


Fig. 3. Life stages of *I. purchasi*. A: crawlers; B: newly settled crawlers; C: second stage, soon after molting; D: third stage; E: adult with its egg sac; F: adult male scale.

TABLE 1
DURATION OF LIFE STAGES OF *Icerya purchasi* DURING DIFFERENT
SEASONS IN RIVERSIDE

Life stage	Duration (days)					
	1967			1968		
	Summer	Fall	Winter	Spring	Summer	Fall
Incubation period.....	22	26	34	28	25	31
Nymph I.....	14	13	18	14	13	19
Nymph II.....	15	16	23	16	16	29
Nymph III.....	14	12	21	16	13	23
Adult.....	32	39	48	33	29	38
Totals.....	97	106	144	107	96	140

TABLE 2
NUMBER OF GENERATIONS OF *Icerya purchasi* AND ITS NATURAL ENEMIES
IN THREE REGIONS OF SOUTHERN CALIFORNIA

Species	Riverside	Palm Springs	Rancho Santa Fe
<i>I. purchasi</i>	3	3	3
<i>R. cardinalis</i>	12	10	8
<i>C. iceryae</i>	8	2	9

dites. Unfertilized haploid eggs become males, which are uncommon.

In the course of these studies, the production of males was observed to occur during the middle part of the summer and early fall. The incidence of males was recorded from samples taken in the three main regions of southern California, but they were more frequently obtained in the desert and interior areas than along the coast. Males were also observed emerging in the "competition cages." Their nymphs are more active than those of the females and were seen moving around until a sheltered place was found to undergo pupation. They spin white cocoons with a cottony secretion. Adult males emerged from these cocoons in 14 to 20 days. The male is about 0.5 cm long, slow moving, and has a pair of well-developed and functional wings (fig. 3F). Copulation was observed to take place, the female responding to the approach of the male by raising its abdomen.

The production of *I. purchasi* males seems to vary from one year to another, as Bodenheimer (1951) suggests. It may also be related to high temperatures, which in some way favor the development of haploid eggs in the scales. A sample of 12 scales taken in Palm Springs in August yielded five males, and another sample of 42 scales from Banning yielded eight males. Samples from coastal areas, taken at about the same time, yielded only very few males out of hundreds of scales. Hughes-Schrader (1930) stated that the sperm of the males may not be functional, but this has not been demonstrated.

Generations of the scale. The first annual generation of *I. purchasi* in California occurs in the spring. By the end of March, the egg sacs have produced their crawlers, and there tends to be a rapid increase of the scale population, which is normally brought under control by the natural enemies in May. The few survivors of the spring attack continue to develop during the summer, and by the end of July or the middle of August, they produce the second generation of crawlers. This is the time at which the most striking upsets of the biological balance due to insecticide treatments seem to occur. In undisturbed orchards, however, the scales are continuously attacked by enemies and are reduced to low levels by the end of October. Again, a few survivors are able to reach maturity and produce a third generation by late November or early December.

There are, thus, about three generations of the scale in California. *Vedalia* has an average of 12 generations a year, and *Cryptochaetum* eight. While the number of generations of the natural enemies may vary to some extent, that of the host seems to be more fixed. This corresponds to what was reported by French, as cited by Kuwana (1922) in relation to the number of generations of the scale in Formosa. The number of generations of *I. purchasi* and its natural enemies, as recorded in the three regions of southern California over almost two years, is presented in table 2 and graphically shown in figure 4.

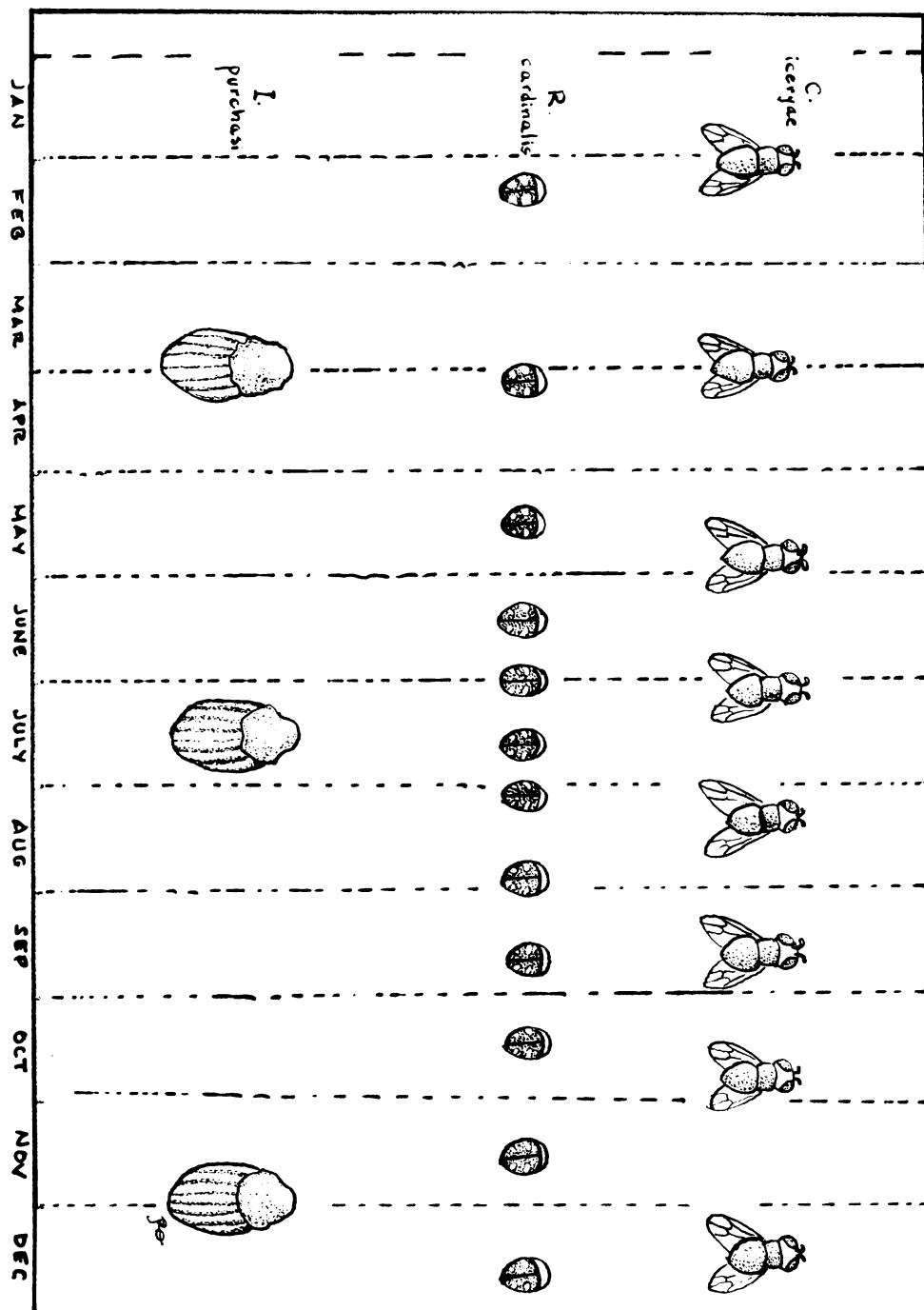


Fig. 4. Generations of *I. purchasi* and its natural enemies in Riverside. The scale has three generations as compared to twelve of its predator, *Rodolia cardinalis*, and eight of its parasite, *Cryp-tochaetum iceryae*.

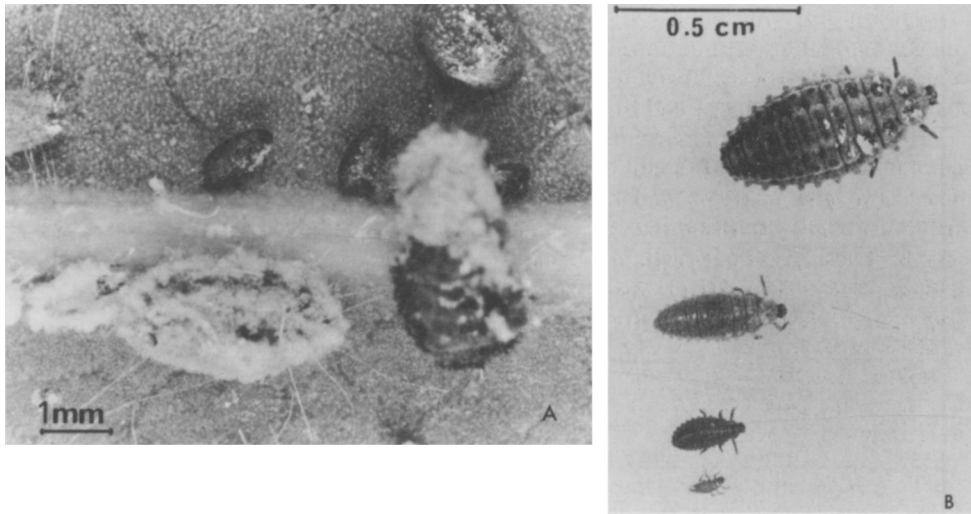


Fig. 5. Life stages of *R. cardinalis*. A: eggs, laid among cottony-cushion scales; B: larval stages.

Biology of *Rodolia cardinalis*

Following its success in controlling *I. purchasi* in California, the vedalia has been imported into many countries (Balakowsky and Molinari, 1930; Delassus, 1923; Jepson, 1939; Bodenheimer, 1930, 1933, 1934, 1951; Kuwana, 1922; De Gregorio, 1916; Wolcott, 1948; Priore, 1963; Simmonds, 1967), where its introduction has in most cases resulted in similar success (Clausen, 1936; DeBach, ed., 1964). In spite of the great acclaim accorded vedalia in California and elsewhere, and except for preliminary studies by Coquillett (1889), a thorough biological study of *R. cardinalis* has not been made in California. This is surprising because it was there that vedalia gained its fame and established the biological control method. In contrast, fairly extensive studies have been made in Israel (Bodenheimer, 1933, 1951), Italy (Priore, 1963), China (Chang and Huang, 1963), and other countries.

Most of the data recorded were obtained in the field, but some observations were also carried out in the laboratory. Although the majority of the observations were made in the River-

side area, some were also made in the other two regions, as will be discussed.

Life cycle. Observations on the life cycle of vedalia in the field were made along with life table studies of the scale. Whenever one or more eggs of the beetle were found on a particular scale or colony of scales, hatching and larval development were recorded for every visit to the orchard. In this way, it was possible to gather data on the life cycle, number of generations, and the like, of vedalia.

After a generally short incubation period, the eggs, which are usually deposited on or near the scales (fig. 5A), hatch, and the larvae start feeding on the scale on or under which the eggs were deposited. The young larvae usually do their feeding under the scale body, and for this reason they may go unnoticed to the casual observer. The older larvae are more conspicuous among the scales because of their habit of feeding on top of them. There are four larval instars (fig. 5B), which have been well described by Coquillett (1889) and Priore (1963). When ready to pupate, the fourth instar larva becomes attached to a leaf or twig by the

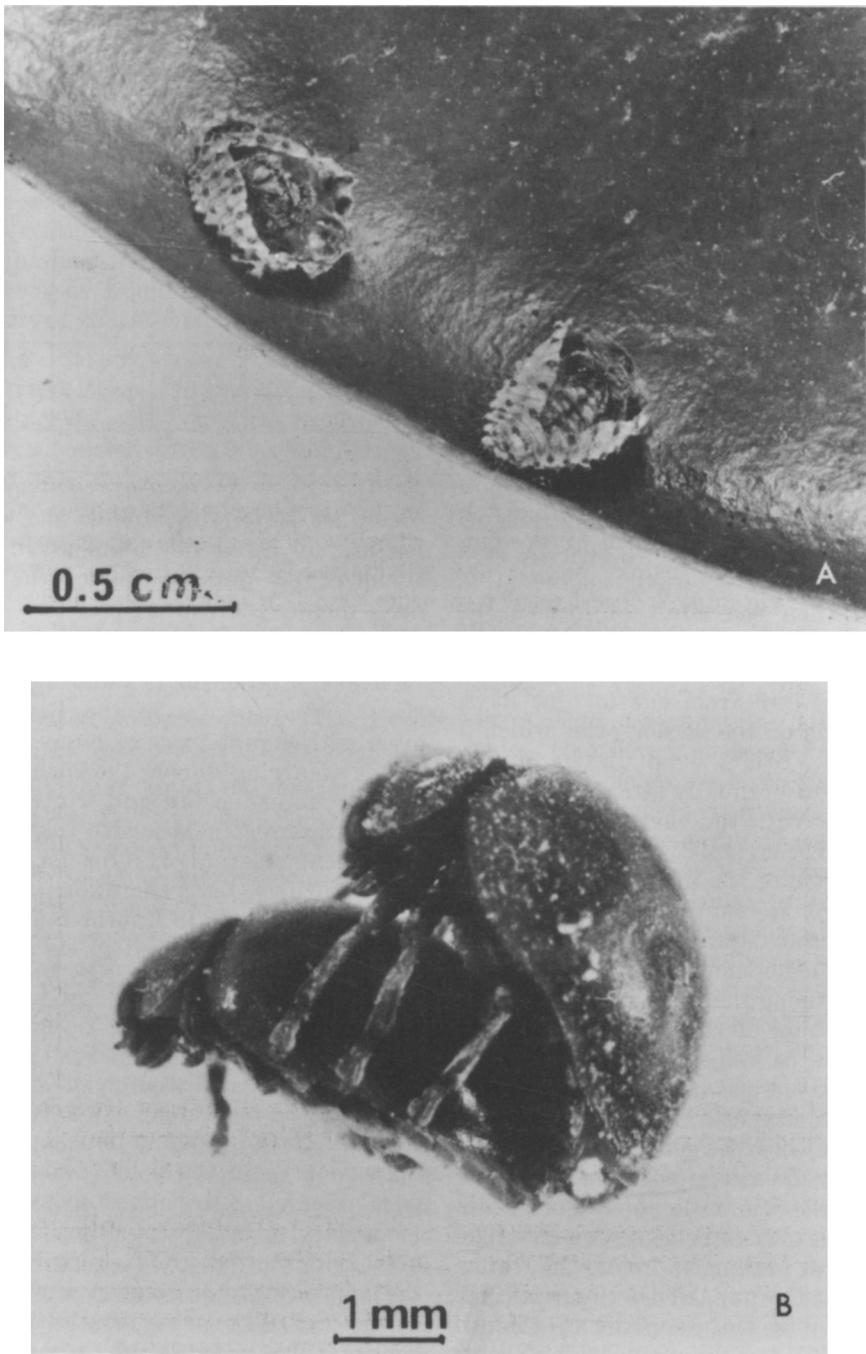


Fig. 6. Life stages of *R. cardinalis*. A: pupae inside the split cast skin of the last larval stage; B: mating pair of vedia.

TABLE 3
DURATION OF LIFE STAGES AND NUMBER OF GENERATIONS OF
Rodolia cardinalis IN SIX DIFFERENT SEASONS IN THE
RIVERSIDE AREA DURING 1967-1968

Stage	Duration (days)					
	Summer	Fall	Winter	Spring	Summer	Fall
Egg.....	2-4	3-7	8-12	5-9	2-3	3-6
Larval stages.....	5-7	8-14	16-24	13-15	5-7	8-14
Pupa.....	5-7	8-11	20-38	7-11	5-7	8-13
Adult remains inside pupal skin.....	1	2-3	5-9	2-3	1	2-3
Totals.....	13-19	21-35	49-83	27-38	13-18	21-36
Number of generations per season.....	4	2	2	4	4	2
Number of generations per year.....12						

pygidium and undergoes its transformation into the pupa, whose outer skin splits in a characteristic manner (fig. 6A). When the adult is formed, its bright red color is seen through the pupal skin. The adult remains inside its pupal case from one to nine days, depending on the season, after which it emerges. Bright red when newly emerged, it gradually attains the darker red color with the characteristic black spots on the elytra.

Duration of the life stages of vedaia is related to temperature and varies from season to season. It is very short during the hot summer months and prolonged during the winter. Table 3 shows the duration of the different stages in Riverside, as well as the number of generations recorded in a year in the same area. From table 3 it is evident that there are about 12 generations per year and that the duration of the life cycle during the winter is about four times as long as that during the summer. The stage most prolonged during the winter is that of the pupa. These figures differ somewhat from those given by Coquillett (1889), but generally coincide with Bodenheimer's (1951).

Observations carried out in the desert and the coast indicated that the duration of the life stages in those areas are

somewhat slower but follow the same pattern of rapid development in the summer and prolongation of the life cycle during the winter.

Number of generations. As shown in table 3, an average of 12 vedaia generations a year occurs in the Riverside area, with almost twice as many generations occurring during the spring and summer as in the fall and winter. The annual figure coincides with that given by Bodenheimer (1951) for Israel. In Palm Springs, ten generations a year were recorded, and in Rancho Santa Fe, the number was reduced to eight. The generations of *I. purchasi* and its enemies in Riverside are represented graphically in figure 4.

Longevity. Cold storage of vedaia adults in the laboratory suggested that the beetle may be able to live more than three months in the field. Two beetles were observed to live almost five months (from November, 1967, to March, 1968) in a field cage at UCR. Longevity in the field seems to be greatest during the winter and early spring months. Bodenheimer (1951), in Israel, recorded a maximum longevity of 178 days for a female and 216 for a male. The shortest longevity occurs during the summer months.

Mating. Adults from field collected pupae started mating soon after emergence in the laboratory (fig. 6B). It is common to see a male attempting copulation with a female pupa, or even tearing the pupal skin and mating with the still soft, almost motionless female. This observation was also repeatedly made in the field, and was reported as early as 1889 by Coquillett. Mating time was observed to last from 20 minutes to one and a half hours in the laboratory.

Oviposition. An average preoviposition period of 48 hours was recorded for eleven females in the laboratory. In the field and in the laboratory the females prefer to lay their eggs on any stage of the scale, with the exception of crawlers. However, eggs may also be laid on the surface of leaves, twigs, or trunks, more or less near the scales (fig. 5A). There is a tendency to lay the eggs under the body of young scales, although they are also placed on top or on the sides. From one to 11 eggs per scale were recorded.

Daily and total oviposition. Two newly emerged vedalia females were placed in separate containers in the laboratory in which citrus leaves infested with scales were introduced. The leaves were removed every 24 hours and oviposition recorded. One of the females oviposited for 44 days and laid a total of 154 eggs. The second female oviposited for 45 days and laid a total of 193 eggs. Daily oviposition ranged from one to 14 eggs. In both cases, there was a relative high initial oviposition, and 50 per cent of the eggs were deposited by the end of 18 days. The first female deposited 75 per cent of its eggs after 27 days; the second female did so after 31 days. The total figures do not greatly differ from those given by Coquillett (1889) in California and Bodenheimer (1951) in Israel, but differ from those (average 119 to 329 eggs per female) obtained by Chang and Huang (1963) in China.

The viability of eggs laid by the two

females mentioned above was also recorded. From 33 to 85 per cent of the eggs hatched. Viability of eggs in the field seems to be lower, as suggested by several observations carried out along with life table studies of *I. purchasi*. When eggs of vedalia were found, they were inspected in subsequent visits to the orchard and their viability was recorded. Under field conditions, only 23 per cent to 42 per cent of eggs hatched in the spring, summer and fall, and only 16 to 33 per cent hatched in the winter. A few of the eggs overwinter and are able to hatch during the spring.

Total progeny. Observations on total F_1 progeny production per female were made in the greenhouse, in which the temperature was $80 \pm 2^\circ\text{F}$ and the relative humidity 65 ± 5 per cent. A *Pittosporum tobira* infested with approximately 700 third-stage scales, and confined in a $2 \times 2 \times 2$ ft sleeve cage, was placed in the greenhouse. One newly emerged vedalia female and a male were introduced in the cage and allowed to reproduce. To avoid overlapping of generations, pupae were removed when they were formed and held in the greenhouse in individual 3-dram vials for emergence. The vials were kept under greenhouse conditions and beetle emergence was recorded. In one test, a total F_1 progeny per female of 76 was obtained, and in a second test, 89.

Feeding characteristics of larvae and adults. Bodenheimer (1951) and Cressman and Dumestre (1930) have given ample data on the feeding of vedalia; however, to develop life tables for *I. purchasi*, we needed to identify the characteristic signs of feeding left in scales that are attacked by vedalia both in the laboratory and in the field. Causes of scale mortality also had to be ascertained.

Recognition of the feeding signs of both larvae and adult vedalia was pos-

sible after repeated observations. The larvae usually, if not always, feed on the underside of the young scales, the latter turning in two or three days from a yellowish color to brown, while assuming a shrunken and dry appearance. Almost the same happens to the new adults and producing scales, with the difference that they gradually curve their posterior end upwards. By this time, the growing larvae of the predator, which may have gone unnoticed, are seen. When vedalia larvae are feeding, or have fed previously, on any stage of the scale, their presence can be detected by their dark gray exuviae.

Adult vedalia feed on the upper surface of the scales, resulting in all stages presenting a ragged appearance. When a colony of the scale is fed on by adult beetles, the tearing of young and adult prey, as well as the reddish excreta of the predators is evident on the leaves or on the scale remains.

Both adult and larvae of vedalia avoid eating scales which contain mature larvae or pupae of *Cryptochaetum*. This observation will be explained and discussed later.

Cold storage of vedalia pupae and adults. Vedalia pupae had been observed to be able to withstand relatively prolonged periods of cold weather in the field and still emerge as adults when the weather warms. Laboratory tests, therefore, were conducted to find out how vedalia pupae can be stored at low temperatures without affecting reproduction. Four hundred pupae were collected in a citrus orchard in which they were especially abundant in January, 1968. These pupae had been exposed to cold weather in the orchard for about three weeks. In order to get pupae of a more or less uniform age, only those which were just beginning to show the typical dorsal splitting of the pupal skin (fig. 6A) were taken. They were

collected while still attached to the leaves and brought to the laboratory.

To avoid injury, the pupae were separated from the leaves by trimming each leaf about 1 cm. around the pupae. Groups of 20 pupae were confined in ten-dram vials covered with screened lids, and all the vials were placed in a $55 \pm 2^\circ\text{F}$ and 50 ± 5 per cent RH cabinet. Every five days one of the vials was removed to room conditions ($80 \pm 2^\circ\text{F}$, 55 ± 5 per cent RH). The per cent of successfully emerged beetles was recorded and the adult beetles were provided scales on which to feed and oviposit. When about 50 eggs were secured, the adults were removed and the hatching of eggs recorded to assess viability. One hundred per cent emergence followed by normal oviposition and egg hatching occurred after 35 days in cold storage. After 48 days of cold storage, only about 50 per cent of the pupae became adults. However, these mated and laid eggs, most of which hatched into larvae which eventually developed into adults. This accords with reports by Bartlett and Lagace (1960). Cold storage of vedalia adults was also tested. Groups of ten newly emerged beetles were placed in 20 separated one-pint carton containers after being fed honey for two days. Honey was provided on excelsior strips in the containers, which were placed in a $60 \pm 2^\circ\text{F}$ and 70 ± 5 per cent RH cabinet.

Every week one of the containers was removed and brought to room temperature. The beetles were offered scales as food and oviposition sites, and the hatching of their eggs recorded. Survival was 100 per cent up to 45 days. Per cent survival declined to 54 per cent after 80 days and was only 15 per cent after 95 days. In all cases, subsequent mating and oviposition occurred. The number of eggs laid was proportional to the period of the cold exposure. Larvae hatched from the eggs and full

development took place in all cases. These results, again corresponding closely to those reported by Bartlett and Lagace (1960), suggest, as these authors do, some practicability in the storage of adult vedalia for periodic colonization purposes.

The experiments on cold storage of pupae and adults indicated that vedalia is probably able to stand the usual low winter temperatures in California without serious adverse effects.

Distribution and phenology. Vedula occurs throughout the range of the scale in California. This corresponds generally to all districts in which citrus trees can survive the winter. The beetle is dominant in the warmer southern desert areas of the state all year. It occurs throughout the year in the Riverside area, along with its competitor, *Cryptochaetum*. In the coastal regions, where the fly is dominant, vedalia is common only during the summer months. Essig (1958) stated that "vedalia has since long passed away" in the San Francisco Bay Area, but a sample taken in that city in the early fall, 1967, yielded one beetle. It was suspected that vedalia tends to move into that region from the interior during the warmer months of the year, as it apparently does along the coast in southern California. In order to check further, a survey was made in the San Francisco Bay Area in late June, 1968. After an unsuccessful search in the Golden Gate Park, a group of infested *Pittosporum tobira* bushes was found by the Municipal Court Building. The only evidence of vedalia was two old pupal skins, probably remaining from a previous spring or summer generation. Many dead scales showed *Cryptochaetum* exit holes, and almost all live ones showed signs of being parasitized. One laboratory-infested *P. tobira* plant had been brought from Riverside and was left at a home

in Marin County. Later, five more plants were sent to the area and left at five different places: Albany, Richmond, Walnut Creek, San Mateo, and Palo Alto. Samples were obtained from those plants in the last part of the summer, and yielded small numbers of vedalia. *Cryptochaetum* was always recovered in large numbers from such samples.

Attributes as a natural enemy. The vedalia has a remarkable ability to find and bring under control isolated small colonies of scale on most of the host plant species upon which it may occur. This high searching capacity has been observed and reported by Coquillett (1889), Kuwana (1922), Bodenheimer (1951), Quayle (1938), Bartlett and Lagace (1960), Priore (1963), and others. All these authors have emphasized that the vedalia, like most coccinellid predators, disperses after almost completely destroying the scale colony. A few surviving scales usually are able to build up a new colony, which will eventually be found again by the adult beetle. The vedalia is highly specific, indeed virtually monophagous, in relation to its prey in California. However, it has been reported to feed on and control other species of monophlebinae scales, as *Icerya seychellarum* Westw. (Moutia and Mamet, 1946; Vesey-Fitzgerald, 1940, 1953). *I. palmeri* (Gonzalez and Rojas, 1966), and *Gueriniella serratulae* Fabr. (Bodenheimer, 1930). The high specificity of the beetle, however, may at times result in its scarcity and even local extinction because of periodic lack of prey.

The great ability of the predator to rapidly increase in number was acclaimed at the time of its first success in California (Coquillett, 1889). Bodenheimer (1934) theorized on the capacity of the beetle to increase in numbers and cause destruction of heavy infestations

of the scale. Another attribute of vedaia is its wide climatic tolerance that enables it to live in almost, if not all, the areas where the scale occurs. However, there are occasional reported failures following its introduction into certain places (Kaussari, 1946), or seasonal failures in others (Bennett and Hughes, 1959). The vedaia has no natural enemies in California, according to Coquillett (1889), Quayle (1938), and Thorpe (1930). Our studies confirmed their observations.

Biology of *Cryptochaetum iceryae*

The group of parasitic flies of the family Cryptochaetidae (*Cryptochetidae* of Stone *et al.*, 1965) showed such remarkable characteristics as to be taken from the Agromyzidae and placed in a separate family (Clausen, 1962). Species of the genus *Cryptochaetum* (*Cryptochetum* of Stone *et al.*, 1965) have been studied by several workers (Bezzi, 1919; Hendel, 1933; Thorpe, 1930, 1934, 1941; Ghesquiere, 1943; Foote and Arnaud, 1958; Sasakawa and Arnaud, 1960). Many of these species have been utilized in attempts to control monophlebinae scales (Caltagirone, 1937; Cortes, 1940; Cortés and Isla, 1964; Bennett, 1968; Bennett and Hughes, 1959; Bedford, 1965). Thorpe (1930) elaborated on the introduction of *C. iceryae* and *C. monophlebi* Skuse into California in 1888, and states that of the two species, only *iceryae* became established.

Although frequently overlooked, the importance of *C. iceryae* as a controlling factor of the cottony-cushion scale in California was emphasized as early as 1889 by Riley, and later by Smith and Compere (1916), Essig (1958), Thorpe (1930), and Bartlett and Lagace (1960). The fly has been successfully introduced in Chile, where it alone reportedly keeps *I. purchasi* under control (Gonzalez and Rojas, 1966), and into Bermuda, where it com-

plements the action of vedaia in keeping the scale under control (Bennett and Hughes, 1959).

The biology of *Cryptochaetum* has been described by Smith and Compere (1916) and worked out in great detail by Thorpe (1930). However, most work reported was done in the laboratory, with only a few notes about the field situation. Field observations on the biology of the fly were needed, therefore, to assess its competitive abilities and measure its relative value as a controlling factor of *I. purchasi*.

Life cycle. The egg (fig. 7A) is deposited by the female inside the host, which is attacked by the fly from the second stage onward. There are four larval stages that last about 20 days, after which the pupa is formed. The pupae remain inside the scale body from which the adults emerge through the host's integument. In the Riverside area, the life cycle of *Cryptochaetum* takes an average of 30 days during the summer and fall. During the winter it may be prolonged for as much as 60 days, and in the spring it lasts about 40 days. Data were obtained both from natural field populations and from the "competition cages" described in Materials and Methods. Results in the coastal areas do not differ much from those in the desert.

Number of generations. In the Riverside area, an average of eight generations a year were recorded. Of these, two or three occur during the summer and about two in each of the other seasons. The same is true of the coastal area. Only two generations occur in the desert, since *Cryptochaetum* disperses during the winter.

Mating. Distinction of sexes is not easy at first glance. In general, the female is larger than the male and has a more robust abdomen (fig. 7B). Thorpe's (1930) observation that the fly needs ample room to behave nor-

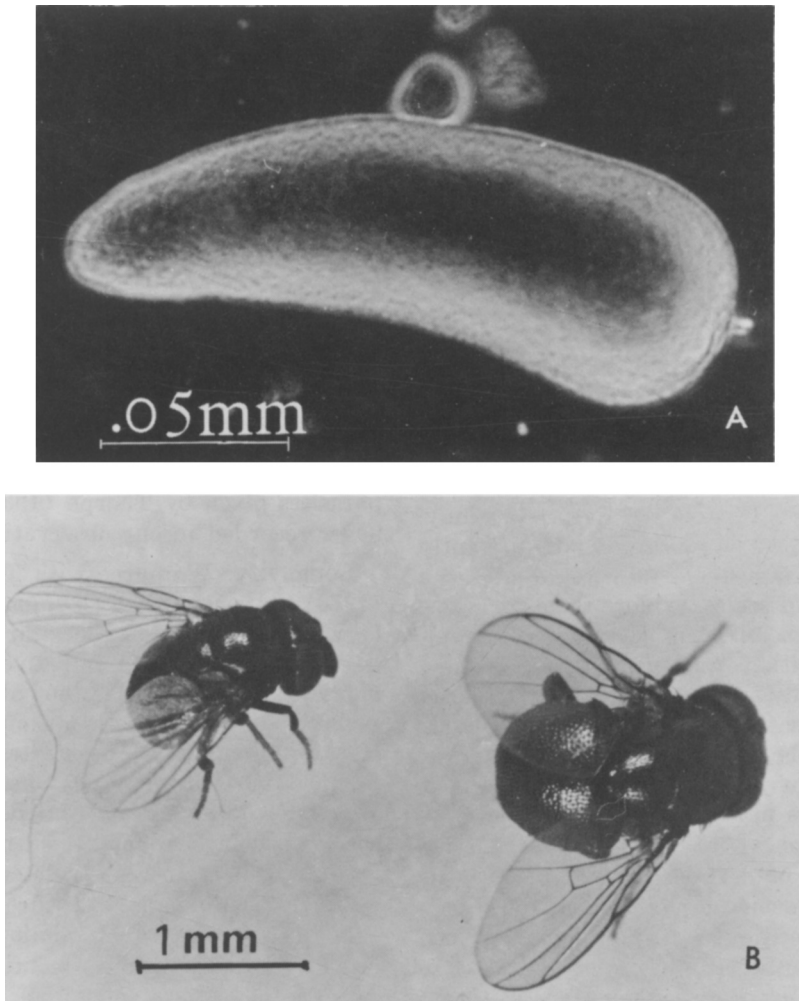


Fig. 7. A: egg of *C. iceryae*; B: *C. iceryae* adults; females (right) are usually larger and have a broader abdomen than the males (left).

mally has been confirmed. For example, in a small $1 \times 1 \times 1$ ft cage, copulation was observed to take place only twice among many flies emerging from field-collected material. Mating was observed more frequently in the larger "competition cages." Copulation was repeatedly observed in the field, and it was usually performed on the foliage of the trees and among the host scales. Both in the laboratory and the field, mating was observed to start soon after emergence. The male was seen to approach the fe-

male, mount, and when copulation was secured, the male made a sudden turn and the flies remained attached in a linear position for 20 to 26 minutes.

Oviposition. Oviposition in a small $1 \times 1 \times 1$ ft cage was observed only in one instance out of 12 trials. A fresh *Pittosporum tobira* twig infested with second- and third-stage scales was introduced into the cage containing parasites. Four minutes later, a female *Cryptochaetum* came to the scales, ex-

plored a few for about one minute and oviposited in one. Oviposition time was quick, taking only about 30 seconds. Dissection of the scale showed that two eggs had been deposited. Further attempts to obtain oviposition in cages less than $7 \times 4 \times 4$ ft resulted in failure. Similar results were reported earlier by Thorpe (1930).

Oviposition was frequently observed in the field. One particularly interesting case involved a swarm of about 100 females actively ovipositing in scales that were abundant on a *Pittosporum tobira* plant at Encinitas. This observation was made in the spring, between 10 and 11 a.m. The temperature was about 68°F, and the day was sunny. The swarm had a rapid and apparently erratic flight. The flies would stop at a group of scales, explore them for a few minutes, and then oviposit (fig. 8A). Oviposition was very rapid, and a single fly was observed to oviposit on seven scales of the same group, one after the other, without much pause. After ovipositing in a group of scales, the flies may remain at rest for up to about one hour without apparent activity, or wander slowly among the scales, sometimes stopping to apparently feed on a drop of honeydew. In other instances, they were observed to suddenly resume their typical flight and move to another oviposition site.

Total progeny. A greenhouse test was made with a *Pittosporum tobira* plant infested with approximately 400 second- and third-stage scales confined in a $7 \times 4 \times 4$ ft sleeve cage. A mating pair of newly emerged *Cryptochaetum* was introduced into the cage and allowed to reproduce. The female was observed actively ovipositing for three days, after which it died. About 30 days later her progeny began emerging. All emerging flies were collected by aspirator and their numbers recorded. The total progeny was 47 in this test, and in

subsequent tests it was found that an average of 52 individuals per female were obtained. The sex ratio in all cases was close to 1:1, as suggested by Thorpe (1930) and Menon (1950).

The number of individuals that develop and emerge from a single scale varies according to the host stage attacked. Small, second-stage scales often are killed by one larval parasite, which usually will not complete development, perhaps due to the inadequate size of the host. Third-stage scales yield from one to four parasites. New adult and producing scales were found to yield up to 11 parasites. The figure of 17 parasites given by Thorpe (1930) was never recorded in our observations.

Longevity. We agree with Thorpe's (1930) statement that *Cryptochaetum* very seldom lives more than three days in captivity, and that it may live longer in the field. The same author also suggests that temperature is an important factor in longevity. In one test, flies confined in 10-dram vials placed in a $62 \pm 2^\circ\text{F}$ and 50 ± 5 per cent RH cabinet with honey for food lived between six and 21 days. It was not determined, however, if prolonged exposure to low temperature affects their ability to reproduce. During four consecutive cold days in the winter (about 50°F) five flies were observed sitting on a caged *Pittosporum tobira* plant without greatly changing their positions during that time. When the temperature increased to about 75 or 80°F, they resumed their activities and lived two more days.

Evidence of *Cryptochaetum* attack. Its attack on the scale may go unnoticed until the emergence holes are evident. Close observation of the scales, however, reveals that when they have been attacked by the fly, their growth is slowed as compared to that of other scales. Their orange-brown color turns

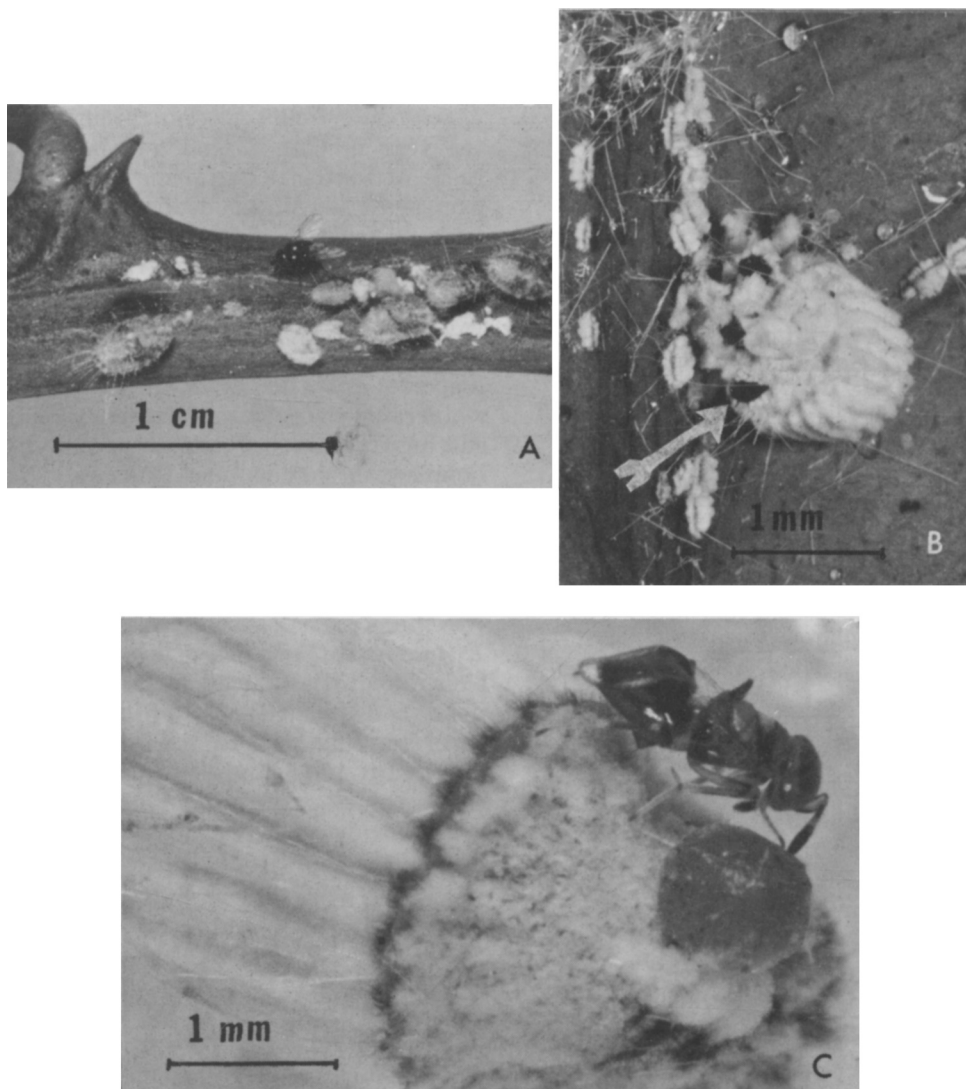


Fig. 8. A: *C. iceryae* female exploring a colony of *I. purchasi*; B: A producing scale showing exit holes of *C. iceryae* (arrow) with crawlers settled nearby; C: *Cheiloneurus inimicus* in the act of stinging a scale parasitized by *Cryptochaetum*.

dull yellowish-gray, the body becomes covered with a yellow powder and later assumes a convex appearance when the mature larvae or pupae of the parasite are formed. In life table studies of the scale, it was very important to recognize the attack of *Cryptochaetum* as soon as possible in order to assess the causes of scale mortality with accuracy.

When *Cryptochaetum* parasitizes a scale which is beginning to form its egg sac, or one that has already formed it, crawler production of the scale continues normally. In the field it is common to find the dead body of such a producing scale showing the exit holes of the fly around its margins. Often young scales are seen settled near the

TABLE 4
OCCURRENCE OF *Cryptochaetum iceryae* BETWEEN THE INTERIOR RIVERSIDE AREA AND THE DESERT DURING 1967 and 1968**

Locality	1967						1968											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Riverside.....	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Beaumont.....	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Banning.....	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cabazon.....	—	—	—	—	—	+	+	+	+	+	+	—	—	—	—	—	—	—
5 mi. east of Cabazon.....	—	—	—	—	—	+	+	+	+	+	—	—	—	—	—	—	—	—
Palm Springs.....	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	—	—	—

** A cross indicates positive rearings; a minus indicates no evidence of *Cryptochaetum*.

mother scale which has been killed by parasitism (fig. 8B).

Distribution and phenology. *Cryptochaetum* was found to occur throughout the year in both coastal and interior areas of southern California but only part of the year in the desert area. Preliminary surveys during mid-summer and fall, 1967, showed it to range only as far as Banning, about midway between Riverside and the desert area. We wanted to know if the fly is able to disperse into the desert when lower temperatures occur. A naturally occurring *I. purchasi* colony had been sampled throughout the summer and fall of 1967 in Palm Springs without ever rearing *Cryptochaetum* from it. No other such colonies could be located between Banning and Palm Springs. It was therefore necessary to place several *Pittosporum tobira* plants infested with scales along Highway 60, between Beaumont and Palm Springs, in order to have sampling stations at intervals between Riverside and the desert. All plants were growing in 5-gallon containers, and each bore about 500 second- and third-stage scales. One plant was left in each of these locations: Beaumont, about five miles west of Banning, and Banning, in home yards; Cabazon, five miles east of Banning, in a small yard at the post office; and the last at a truck weighing station, about five miles east of Cabazon. Samples of about 20 scales were taken every two weeks from all plants, including the one from Palm Springs, and brought to the laboratory. The results are summarized in table 4.

These data indicate that *Cryptochaetum*, contrary to prevailing belief, is able to disperse at least as far as from Banning to Palm Springs during the winter months. As the summer months advance, it gradually disappears from Palm Springs to the Banning area. According to B. R. Bartlett, C. A. Fleschner, and T. F. Leigh (separate personal

communications), the fly can be recovered in the Central Valley during the winter months but not the summer months. It is possible that the fly is able to disperse into those areas as it does in the southern California desert. It is abundant in the coastal areas of Ventura, Santa Barbara, and San Luis Obispo counties. These coastal areas are like refuges, where the fly has its optimal habitat and from which it always can disperse into the interior valleys.

Cold storage of immature stages. A field-collected *Pittosporum tobira* branch with many parasitized *I. purchasi* which showed the presence of young and mature larvae, as well as pupae, of the fly, was placed in a 55°F and 70 per cent RH cabinet. Every week about 20 scales were removed from cold storage and placed in a container which was kept at room temperature (80°F). *Cryptochaetum* emerged from scales previously subjected to low temperature for up to six weeks. These parasites, when confined in a large cage with scale-infested plants, oviposited very actively, and a normal number of progeny was obtained.

Attributes as a natural enemy. Thorpe (1930) made a comparison of the biological characteristics of both *vedalia* and *Cryptochaetum*, and suggested that the fly may be equally effective in controlling the host scale, an assumption that was made earlier by Smith and Compere (1916). From life table studies, survey work, and biological studies, *Cryptochaetum* was found to possess several qualities that make it an effective enemy capable of competing well with *vedalia*, and even dominating over it in coastal areas. The fly is highly specific in regard to its host, just as the beetle is. It differs in attacking scales from the second stage onward. As already pointed out, parasitized adult scales with egg sacs are almost always able to produce crawlers.

This permits the redevelopment of new small colonies of the scales, which provide food for more parasites and permits localized continuity. In this way, the fly is able to maintain itself in small numbers in spite of general scarcity of the scale. *Cryptochaetum* is well able to tolerate rather low temperatures as already shown. This adaptation permits it to maintain the scale at low population levels in the cooler coastal areas. As pointed out by Thorpe (1930), low humidity is probably a critical factor for the fly. This, along with high summer temperatures, may limit its permanent establishment in the desert areas.

Observations in the field have indicated that *Cryptochaetum* is often able to find small isolated colonies of the scale before *vedalia* does, as was suggested by Thorpe (1930). We have also observed that when a scale-infested laboratory plant is placed in the field, the parasites often will be seen exploring the plant within two hours, especially on cool, but sunny, days. These observations raised the question as to whether *Cryptochaetum* is attracted to the scales by odor (e.g., a pheromone) or by the host plant or both. A simple experiment was designed to explore this. *Pittosporum tobira* branches, heavily infested with scales, were cut into 10 cm pieces which were carefully placed individually in an insect-tight screened plastic cylinder (50 mesh/cm²). A check contained a *P. tobira* twig without scales, and a third test cylinder was left empty. Two replicates of each test were used. The cylinders were placed in the open on the roof of a three-story building at the U.C. Riverside campus so that they were isolated from immediate sources of *Cryptochaetum*. Tanglefoot stripes were smeared on the sides of the cylinders to trap any visiting parasites and were inspected several times a day. *Cryptochaetum* flies were never seen coming to any of the cylinders, nor were any captured in the

tanglefoot. The flies, however, were known to be active in infested plants about 40 yards away.

Since it appeared that odor did not attract parasites over this distance, if at all, the test was carried further by placing a scale-free *P. tobira* plant on the building's roof, where the cylinders had been exposed for about one week. Within three hours, four *Cryptochaetum* were seen flying around and exploring the plant. This is a remarkable feat, if typical. These preliminary tests suggest that the parasites are attracted to the host plant rather than to the host itself, a fact that has been demonstrated by other workers with other insects (Pickard and Rubaud, 1914; Cushman, 1926; Salt, 1935; Laing, 1937; Monteith, 1958).

The ability of *Cryptochaetum* to increase in numbers must be considerable, as rearing data have shown. Dissections of females showed that most of them contained around 200 eggs in their ovarioles, an approximate average already indicated by Smith and Compere (1916), Thorpe (1930), and Menon (1950).

No report has been found in the literature showing any unfavorable effect of a host plant on development of *Cryptochaetum* in the host insect. While plants such as *Cocculus laurifolius* were proven to make cottony-cushion scale unsuitable for vernalia, they did not affect *Cryptochaetum*.

Argentine ants, *Iridomyrmex humilis* Mayr, and other species of ants, can be very aggressive toward the fly, and affect its activities more than those of vernalia (see p. 670-71).

It is also important to emphasize that scales containing mature larvae or pupae of *Cryptochaetum* are not eaten by vernalia. This is considered to be a strong attribute of the fly in its competition with the beetle (see p. 673-74).

Thorpe (1930) stated that *Cryptochaetum iceryae* does not have natural enemies in California, although it has

them in Australia. However, we have found that the fly may occasionally be attacked by hyperparasites. Rearings from samples of scales that were abundant on *Cocculus laurifolius* in Soboba Springs occasionally yielded one or two *Cheiloneurus inimicus* Compere (identified by Dr. D. Rosen). Since no soft scales were seen on the plant, it was suspected that these encyrtids were hyperparasites that had attacked *Cryptochaetum*. They were tested by offering them scales that were known to be parasitized by *Cryptochaetum*. The encyrtids responded immediately to the presence of the scales and began to explore and sting them (fig. 8C). Their mode of oviposition was rather quick, and it would last no more than two minutes. A single scale was seen to be stung by the same parasite at five different points. The life cycle of the hyperparasites ranged from 14 to 18 days in the laboratory. As far as is known, this is the first report of the rearing of *Cheiloneurus inimicus* from *Icerya purchasi* in California or elsewhere. Wolcott (1948) reported *C. pulvinariae* Dozier as having been reared from *I. purchasi* and *I. monserattensis* Riley & How. in Puerto Rico, but did not indicate its primary or secondary status. The primary parasite of *Icerya* in Puerto Rico is *Syneura cocciphila* Coq., a parasitic phorid fly, out of which the encyrtids may possibly have been reared by Wolcott.

The hyperparasitic *Cheiloneurus inimicus* were obtained from samples taken beginning September, 1968, and they were more frequently reared as the fall season advanced. Their attacks on the fly do not prevent the fly's ability to maintain the scale under control. Probably not more than 0.1 per cent of the immature *Cryptochaetum* were attacked. It is probable that *Cryptochaetum* is not a favored host among the many that may be utilized by *Cheiloneurus inimicus*.

POPULATION REGULATION OF *Icerya purchasi* BY ITS NATURAL ENEMIES

This outstanding case of biological control involving two natural enemies of a single pest has not been studied in sufficient detail in California. Most conclusions are based on observations, and population studies are virtually non-existent. An adequate quantitative and experimental evaluation of the degree of control exerted by the two natural enemies in various habitats has not been done. In order to obtain that information we made a field census and collected data for a life table, along with other experimental studies. The objective was to compare the degree to which each enemy regulates scale populations in the various districts and to evaluate the effects of adverse or modifying factors such as ants, host plants, climate, and the like, on the relative efficacy of the natural enemies. Competition between the enemies of the scale is recognized as a factor, but this will be analyzed later.

The efficacy of vedalia has been most striking in recent years when upsets of the cottony-cushion scale have occurred due to the application of DDT and other sprays. The beetle has proved to be sensitive to several pesticides including HCN (Branigan, 1915), rotenone (DeBach, 1947), DDT (DeBach and Bartlett, 1951), and malathion (Carman, Elmer, and Ewart, 1954). The use of these and other chemicals may cause outbreaks and prevent or delay control by vedalia. Two chemically caused upsets have been observed in the course of these studies. One took place in a grapefruit orchard in Sunnymead during the summer of 1967 after a methyl-parathion spray had been applied in the spring. The vedalia was not found in that orchard until October, and control was only attained by the end of the year. The other upset was observed in another grapefruit orchard in Hemet,

in the fall of 1968, as the result of the same pesticide having been used in the previous spring. During the course of these studies, several requests for vedalia were received from growers troubled by upsets in different areas of southern California and the Central Valley.

Survey and periodic census of the scale and its natural enemies

A survey of the cottony-cushion scale and its natural enemies was begun in the winter, 1967, and terminated in the fall, 1968, covering about a two-year period. As explained in Materials and Methods, colonies of the scale were located, inspected and sampled periodically in order to obtain a broad picture of the distribution and relative abundance of *Icerya purchasi*, *Rodolia* and *Cryptochaetum* in various areas and seasons. The number of scales in the sample, the presence of ants, and other ecological data were recorded. Each sample was placed in a paper bag and brought to the laboratory, where it was confined in a rearing cage to await emergence of parasites and predators. When all the natural enemies had emerged, they were counted and recorded along with other data.

The survey work was particularly helpful in developing a general understanding of the distribution, phenology, and relative abundance of the natural enemies of the cottony-cushion scale. It also provided live material for experimental work inasmuch as the sample material could be used for other purposes once counts were made. Thus, scale crawlers became available for host plant infestations, live *Rodolia cardinalis* and *Cryptochaetum iceryae* for competition experiments, and the like.

Census errors may arise if small general predators or scavengers destroy

some of the developing natural enemies before they emerge. To check such errors, individual rearings of vedalia and *Cryptochaetum* pupae were made, as well as random checking of pupal material of both. No evidence of predatory or scavenger interference in the sampling results was found. Pupae of vedalia showed a high per cent emergence with no evidence of being parasitized. A low percentage of *Cryptochaetum* pupae were attacked by the hyperparasite *Cheiloneurus inimicus*.

A total of 389 periodic rearing samples of cottony-cushion scale were obtained in about two years of survey work. They were collected from 19 different host plant species in 42 different localities. Some colonies were sampled several times, at different intervals, especially if they proved valuable in furnishing data relating to the competitive interactions of the natural enemies or other biological relationships. Data from the survey revealed interesting and valuable information on the distribution of the pest and its enemies, host plant effects on them, and competitive abilities of the predators. The results of the periodic census are summarized in table 5.

Desert area (Palm Springs). The infestation of cottony-cushion scale selected for study was just beginning to increase in mid-July, 1967, on a group of *Pittosporum tobira* bushes at a home in Palm Springs. No natural enemies were observed for about two weeks, then the vedalia beetle slowly began to reproduce. The scale colony, however, kept increasing in the presence of beetles, perhaps because Argentine ants, *Iridomyrmex humilis*, were attending the scales. The ants may have been responsible for the initial lag in the control of the scales, as the experiments reported herewith suggest. The beetles, however, eventually increased to sufficiently high levels to achieve control by

the end of November. The cooler winter temperatures then apparently slowed down the activities of vedalia, and the scale colony was slowly recovering by the middle of February, 1968. *Cryptochaetum* was observed to be present in January and was reared from small weekly samples during March, April, and the first week of May. Vedula larvae were present in small numbers, but adults were not seen until the middle of April, when vedalia again started to destroy the scales at a more rapid rate.

Interior area (Riverside). As table 5 shows, both species of natural enemies are commonly found in this area throughout the year. In general, their relative abundance at a given time appears to be related to seasonal climatic conditions. However, the success of either one in a given colony may depend on its ability to find the scale colony before the other one does. Searching ability is remarkable in both natural enemies. Two colonies were studied. The first was found on a *Pittosporum tobira* plant in a park in downtown Riverside in mid-July, 1967. No natural enemies were observed at that time. Two weeks later, adult *Cryptochaetum* emerged, which meant that the fly, whose life cycle averages 30 days in the summer, had found the colony at least one month before. For the following three months, only *Cryptochaetum* was reared from samples taken from this plant. Vedula was not recovered from this colony until the middle of November. Contrasting results were obtained during the same general period on another *Pittosporum tobira* plant about half a mile away. This colony was found by vedalia long before *Cryptochaetum* arrived. Sampling was started in late July, 1967, and vedalia was the only natural enemy recovered during the next three months. The fly was seen flying near the bush in mid-August, but it was not recovered from the scales until late October. Then,

TABLE 5
DISTRIBUTION AND RELATIVE ABUNDANCE OF SCALES, OF *Rodolia cardinalis* AND *Cryptochaetum iceryae* IN THREE CLIMATIC REGIONS OF SOUTHERN CALIFORNIA DURING DIFFERENT SEASONS (1967 AND 1968)*

Region and locality	Host plant	Number of predator and prey											
		Summer			Fall			Winter			Spring		
		Scales	Vedalia	<i>Cryptochaetum</i>	Scales	Vedalia	<i>Cryptochaetum</i>	Scales	Vedalia	<i>Cryptochaetum</i>	Scales	Vedalia	<i>Cryptochaetum</i>
Interior	<i>Pittosporum tobira</i>	578	0	307	120	119	1050	325	12	284	50	3	22
	<i>Nandina domestica</i>	400	8	163	800	105	513	200	5	103	38	4	21
	<i>P. tobira</i>	1200	0	228	250	34	741	1075	43	399	100	1	42
	Colton.....	28	0	0	550	0	10	1300	82	1547	115	134	323
	<i>P. tobira</i>	101	3	40	80	44	1	200	22	86	115	156	612
	<i>Citrus aurantium</i>	83	7	19	121	16	27	48	9	14	—	—	—
Totals		2410	18	757	1921	318	2342	3148	173	2433	418	298	1020
Desert	<i>C. aurantium</i>	188	12	0	210	28	0	13	0	0	36	14	0
	<i>P. tobira</i>	306	50	0	34	3	0	80	0	19	40	5	2
	5 mi. West of Cabazon	140	13	0	70	9	0	20	0	6	10	2	0
	<i>P. tobira</i>	180	16	0	50	3	0	70	2	7	25	2	6
	Totals	814	91	0	364	43	0	183	2	32	111	23	8
Coast	<i>P. tobira</i>	430	4	63	320	7	247	1200	9	910	220	10	18
	<i>C. aurantium</i>	60	0	0	140	192	43	825	4	1310	—	—	—
	<i>P. tobira</i>	920	41	660	1200	18	344	900	0	3880	120	0	32
	<i>C. aurantium</i>	500	0	578	400	6	541	120	2	20	54	4	169
	<i>C. aurantium</i>	348	0	146	223	2	385	418	0	560	118	0	26
Totals		2258	45	1447	2283	225	1560	3463	15	6680	512	14	245

* Scales were collected ; vedalia and *Cryptochaetum* were reared.

after the scales were greatly reduced and vernalia had dispersed, a few *Cryptochaetum* were reared. Similar cases were observed on the U.C. Riverside campus and in Loma Linda, in which a "monopoly" of either the beetle or the fly occurred.

Coastal area (Encinitas). A colony of *Icerya purchasi* on a *Pittosporum tobira* plant was found in a home yard at Encinitas, about four blocks from the beach in mid-August, 1967. At that time there were no apparent signs of natural enemies. One week later, *Cryptochaetum* was seen actively flying and ovipositing. Weekly samples of the scales yielded parasites by the middle of September, and kept yielding them until the end of November, when the colony was practically destroyed. Vernalia was first seen in early September. It reproduced only in small numbers, then vanished by the end of October. At this time, most of the scales had been parasitized by *Cryptochaetum*, and the fly was at the peak of its emergence. The control of this colony must be ascribed virtually to the fly alone. In several other places, including San Clemente, South Laguna, and El Segundo, similar results were obtained.

The survey, periodic censuses, and case history studies provided ample data to conclude that vernalia is strongly dominant in the desert area and is almost entirely responsible for control of the scale there. The fly, on the other hand, strongly dominates the coastal areas, where the somewhat more climatically tolerant vernalia manages to persist in small numbers throughout the year, increasing a little during the late summer and fall. The two enemies are common the year round in the interior area, so that competition between them is severe. In spite of the evidently rather evenly matched competition between the two natural enemies of the scale in the interior, the host, as shown

by the survey work, is maintained under control at low population densities, which is contrary to what would be expected if the hypothesis of Turnbull and Chant (1961) is accepted.

During the cold months, the control of the host by vernalia may be handicapped by the weather. *Cryptochaetum* appears to do best during the cool part of the year. In some instances, it may be practical to make periodic releases of the fly during the winter months to suppress insecticide-induced cottony-cushion scale upsets that occur in the interior or desert areas, as was suggested by Bartlett and Lagace (1960).

The survey showed that vernalia, which was reported to be excluded from the Bay Area (Essig, 1958), occurs there during the summer and fall months, although in small numbers. On the other hand, there are indications that *Cryptochaetum* may invade the Central Valley during the winter, just as it is able to get into the lower desert areas during the same period.

Life table studies and density estimations

The Biological Control Grove at UCR, an orchard in Rancho Santa Fe, and a small backyard orchard in Palm Springs, provided the sites for observations on *Icerya purchasi* that led to the development of life tables of the scale in these three regions of southern California. The groves had been unsprayed for many years, so that their condition was close to natural.

A sample method was devised to estimate the density of the scales in a grove. All the trees to be sampled were of about the same age. A timer was set to ring at the end of five minutes, during which time one tree was inspected by walking around it, slowly, turning leaves and counting the scales seen. Twenty trees were inspected at random in every orchard at the beginning of each season, and an average of scales

TABLE 6
AVERAGE NUMBER OF SCALES FOUND PER TREE IN FIVE-MINUTE SEASONAL
SEARCHES IN 20 TREES IN EACH OF THREE DIFFERENT
REGIONS IN SOUTHERN CALIFORNIA

Season and year	Average of scale density per tree		
	Riverside	Rancho Santa Fe	Palm Springs
Summer, 1967.....	1.70**
Fall, 1967.....	1.75	1.80	1.50
Winter, 1968.....	2.00	1.90	2.05
Spring, 1968.....	0.90	1.10	0.90
Summer, 1968.....	0.70	0.60	0.70
Fall, 1968.....	1.95	1.70	1.40

* ... = no measure taken.

counted per five minutes was taken as an index of scale density. An estimation of the number of leaves inspected in five minutes was also made in order to check the uniformity of the method. Five minutes' inspection of leaves was made in 40 trees at the Biological Control Grove. The minimum of leaves checked was 70, the maximum 111. From all trees an average of 99.85 leaves was obtained, so that it can be said that 100 leaves per tree were inspected in five minutes. The figures obtained for all seasons and regions are summarized in table 6 and are represented graphically in figure 9. The figures presented in table 6 show that the density of the scale is maintained at a very low level in the three climatic regions of southern California studied. Results showed that densities tended to be lower in the summer, then gradually increased and reached a peak in the winter, declining again during the next spring and summer.

Assessment of mortality factors:

In tagged individual scales. One hundred individual scales were tagged in the same groves in each area at the beginning of each season and inspected as often as possible. Those at the Biological Control Grove were inspected every other day, and the ones on the coast and in the desert once a week, or even

twice when possible. The experience gained by previous trials and observations made it possible to determine with reasonable accuracy the cause of mortality for each individual scale. The number of scales lost in any particular area or season was negligible (no more than 4 per cent), which makes these observations very precise. The criteria used to recognize the attack of *vedalia* and *Cryptochaetum* have been explained. This previous experience was particularly valuable in the coastal and desert regions, which for reasons of distance could not be visited as often as the Riverside plot. The results are presented in figure 10 and tables 7, 8 and 9.

Tables 7, 8 and 9 reveal two interesting aspects in the pattern of control of the cottony-cushion scale: First, during the summer in all regions more scales were able to escape attack and produce crawlers. This helps explain the higher density indexes (table 6) obtained during the fall. Second, in any season the total mortality of the scales caused by its two natural enemies combined did not vary appreciably from one region to another. Statistical analysis showed no significant differences among total enemy-caused mortality in the three regions at any given season. Neither were the differences significant among the numbers of scales that escape attack

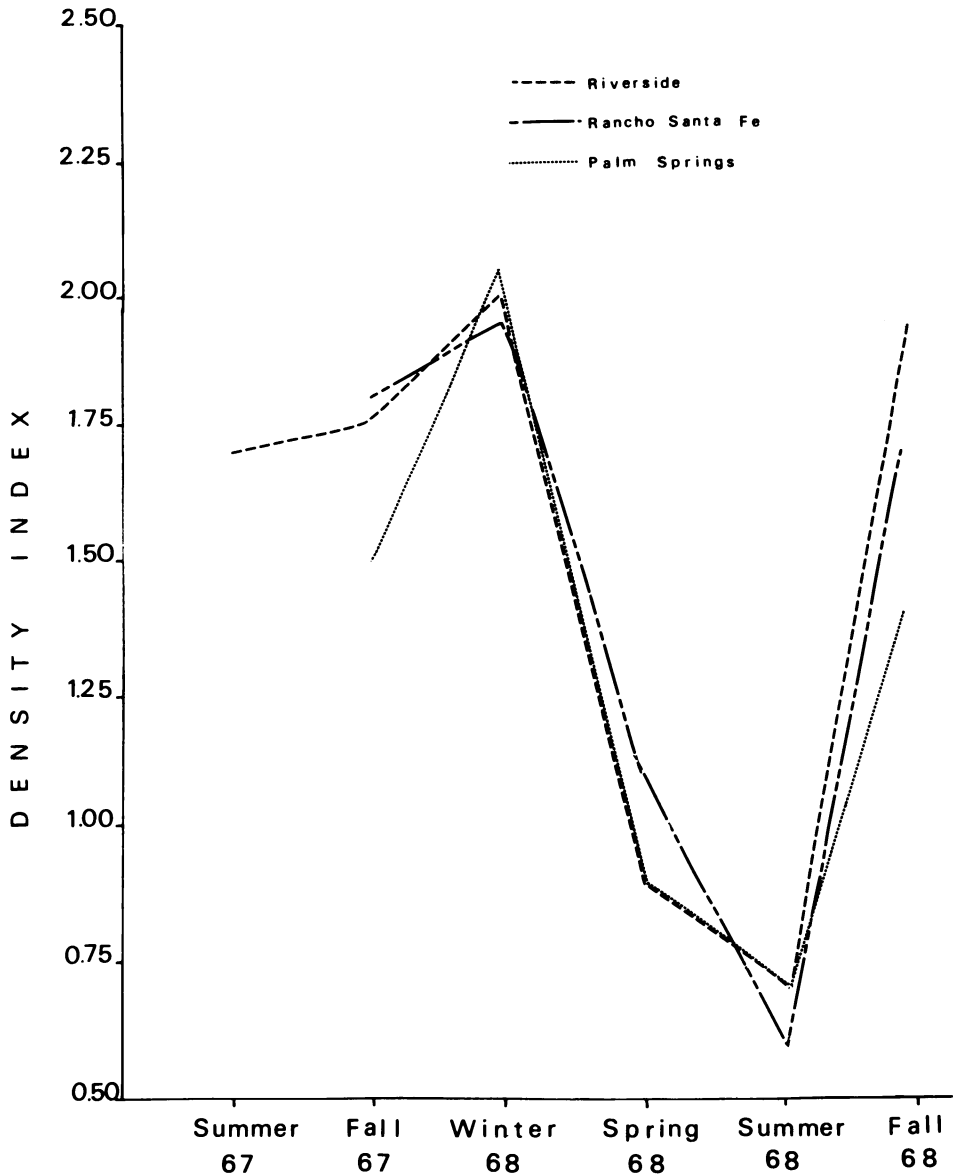


Fig. 9. Population density indexes (average number of *I. purchasi* found in five-minute search per tree) in different seasons and different regions of southern California.

in the three regions under the same circumstances. All this supports previous indications that in the interior area, where the two natural enemies compete rather intensely, they exert just as good control over the scale as they do essentially separately in the desert (mainly

vedalia) and in the coast (mainly *Cryptochaetum*). It is noteworthy to compare the mortality at Riverside with that at Palm Springs during the winter and spring, for it is at this time that *Cryptochaetum* migrates into the desert and competes for the prey with the

TABLE 7

FATES OF 500 INDIVIDUALLY TAGGED *Icerya purchasi* IN THE
RIVERSIDE AREA—100 IN EACH OF FIVE DIFFERENT SEASONS

Fate of <i>I. purchasi</i>	Fall 1967	Winter 1968	Spring 1968	Summer 1968	Fall 1968
Produced crawlers.....	11	3	2	19	9
Eaten by vedalia.....	59	48	16	42	58
Parasitized by fly.....	22	43	78	32	26
Dead, unknown causes.....	4	4	2	4	4
Lost.....	4	2	2	3	3

TABLE 8

FATES OF 500 INDIVIDUALLY TAGGED *Icerya purchasi* IN RANCHO
SANTA FE—100 IN EACH OF FIVE DIFFERENT SEASONS

Fate of <i>I. purchasi</i>	Fall 1967	Winter 1968	Spring 1968	Summer 1968	Fall 1968
Produced crawlers.....	7	4	2	16	9
Eaten by vedalia.....	9	3	4	10	12
Parasitized by fly.....	78	85	91	72	76
Dead, unknown causes.....	3	4	2	2	2
Lost.....	3	4	1	0	1

TABLE 9

FATES OF 500 INDIVIDUALLY TAGGED *Icerya purchasi* IN PALM
SPRINGS—100 IN EACH OF FIVE DIFFERENT SEASONS

Fate of <i>I. purchasi</i>	Fall 1967	Winter 1968	Spring 1968	Summer 1968	Fall 1968
Produced crawlers.....	4	6	5	17	4
Eaten by vedalia.....	88	76	78	74	91
Parasitized by fly.....	3	13	12	0	0
Dead, unknown causes.....	3	2	4	5	3
Lost.....	2	3	1	4	2

dominant vedalia. Also of interest is a comparison between Riverside and Rancho Santa Fe during the summer and fall, seasons during which vedalia obtains a larger share of the scale in competition with *Cryptochaetum*; there were no significant differences.

These data also show that in the interior area, competition between the two enemies seems to be nearly balanced. In the summer, vedalia takes a little larger proportion of prey than *Cryptochaetum*. In the fall, the beetle becomes more dominant, probably due to weather conditions being more suitable to it. During the winter, vedalia still takes more prey

than *Cryptochaetum* but only by a small margin. As the winter advances, approximately an equal number of prey is taken by each. By spring, *Cryptochaetum* becomes dominant, again probably because weather conditions at this time are more suitable to it than to vedalia. The beetle becomes more active in the late spring as temperature increases, but by this time most of the scales have been taken by the fly.

On the coast, these interrelations are quite different. Here, the fly always is dominant and increasingly so in relation to the more rigorous temperatures. It practically displaces vedalia com-

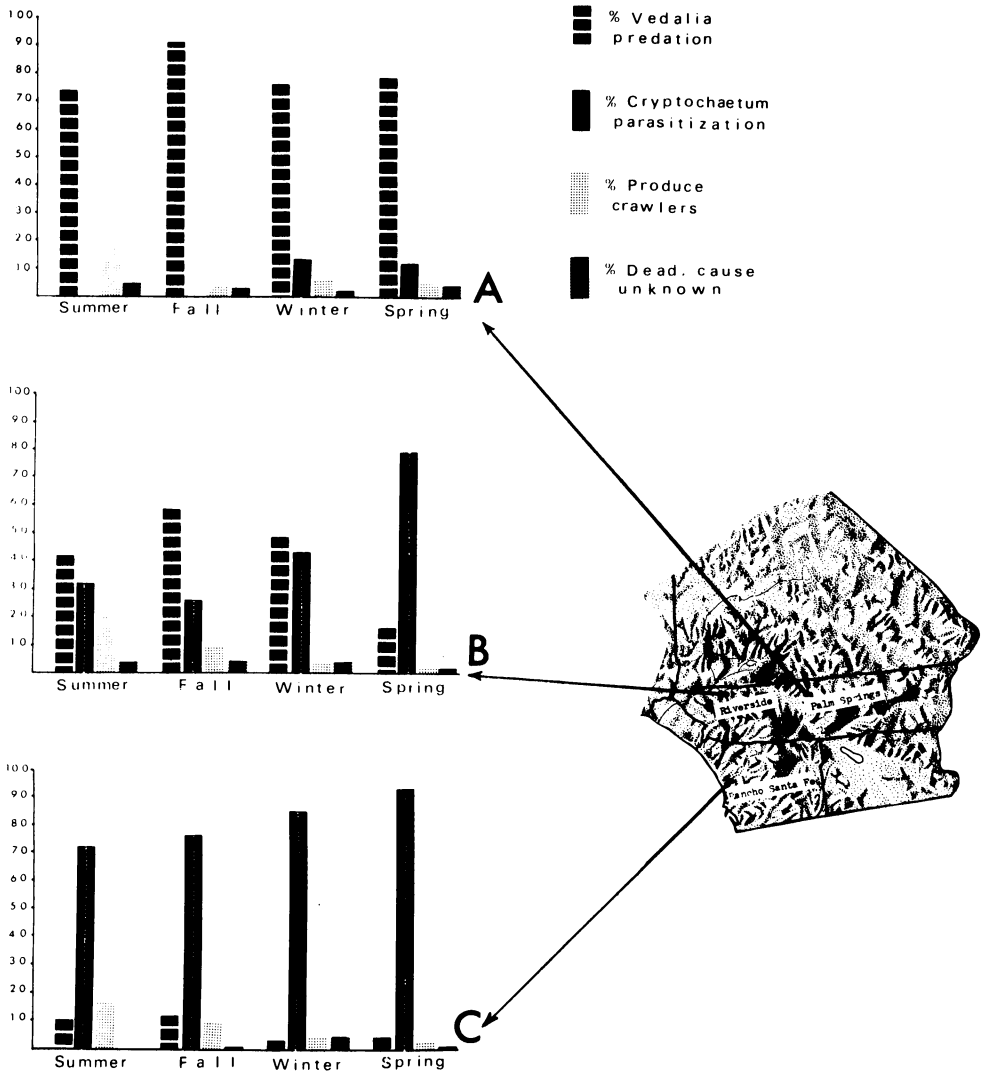


Fig. 10. The mortality and survival of *I. purchasi* during different seasons and in different regions of southern California. A: desert (Palm Springs); B: interior (Riverside); C: coast (Rancho Santa Fe).

pletely in the winter and early spring. *Vredalia* does, however, persist in coastal environments during the whole year. It becomes most common during the summer and fall, but the overall control of the scale, nevertheless, is overwhelmingly exerted by *Cryptochaetum*.

Conditions in the desert areas are re-

versed from those on the coast. *Vredalia* is completely dominant and regulative all year, and *Cryptochaetum* only moves into those areas during a relatively short period from late fall to early spring when conditions are more favorable.

Regardless of their relative domi-

TABLE 10
DAYS TAKEN BY NATURAL ENEMIES
TO BRING *Icerya purchasi* UNDER CON-
TROL IN THREE REGIONS AC-
CORDING TO SEASON

Region	Summer	Fall	Winter	Spring
Coast.....	50	46	65	49
Interior.....	47	49	58	53
Desert.....	51	54	59	51

nance in the different regions, the two natural enemies combined cause similar mortalities of the scale. In the Riverside area, the average per cent of prey destroyed ranged from 74 per cent in the summer to 94 per cent in the spring. In the desert, the respective figures are 74 to 90 per cent, and on the coast, from 82 to 95 per cent.

The time needed by the natural enemies to bring the scale under control in the study plots in each district is shown in table 10.

In tagged colonies of scales. Entire colonies of scales were tagged in order to ascertain how their mortality and survival differed from the tagged individuals (table 9). During each season, egg sacs were located, and the total production of crawlers was recorded for 20 scales selected at random in the Biological Control Grove of U.C. Riverside. When the crawlers settled along leaf veins and small branches, a sketch of the colony was made, and each individual scale was assigned a number. The 20 colonies were inspected every other day, or even daily, when it was possible. When the number of young scales was relatively small, the fate of the individuals could be followed with great accuracy. Larger colonies were more difficult to work with, and individuals often moved when molting from one stage to another. However, the numbers of scales lost was low, and an assessment of mortality was made with a reasonable degree of accuracy. The results of these

observations are presented in table 11.

It was impractical to determine the initial number of crawlers produced by the scales in the field. However, 17 scales with egg sacs full of unhatched eggs were collected in the U.C. grove, brought to the laboratory, and confined in separate containers at room temperature ($80 \pm 2^\circ\text{F}$). They produced an average of 197 crawlers (minimum, 178; maximum, 223). This figure is close to that given by Kuwana (1922) but differs from the ones recorded by Bodenheimer (1951).

Assuming that about 200 crawlers are produced per female, the figures in table 11 show that a large number of crawlers failed to settle (compared with those from the laboratory rearings), probably because they were blown off by the wind, washed off by rains, or otherwise killed, depending on the prevalent climate at a particular season. Predation was obviously another cause. In the test reported in the section, Bioecological Studies, only about 12 per cent of the crawlers settled on citrus plants in the field.

If we assume that an average of 200 crawlers is produced by each female, then 4,000 crawlers were produced by the 20 females observed. The totals and percentages in table 11 show that the per cent crawlers settled was less than 50 in the summer and less than 40 in other seasons. During the summer, less than 50 per cent of the first stage larvae which settled attained the second stage. This mortality was largely due to vedalia attack. The second-stage scales were subjected to a heavier attack by the beetle, along with increasing *Cryptochaetum* parasitization. Only 3.2 per cent of the larvae which attained the second stage reached the third stage. This represents a survival of only 0.8 per cent of the original 4,000 hatched crawlers, or 1.5 per cent of the 1,894 settled crawlers. At such low densities,

TABLE 11
SEASONAL MORTALITY BY STAGES OF *Icerya purchasi* IN RIVERSIDE

Season	Stage	No. individuals		Survivors	Mortality	
		Initially	Finally		Over previous stage	Cumulative
Summer	Crawlers.....	4,000*	1,894	Per cent 47.3	Per cent 52.7	Per cent 52.7
	Settled crawlers to second instar.....	1,894	903	47.6	52.4	77.6
	Second instar to third instar.....	903	29	3.2	96.8	99.2
	Third instar to egg sac.....	29	7	24.1	75.9	99.8
Fall	Crawlers.....	4,000*	1,465	36.6	63.4	63.4
	Settled crawlers to second instar.....	1,465	415	28.3	71.7	89.6
	Second instar to third instar.....	415	37	8.9	91.9	99.0
	Third instar to egg sac.....	37	3	8.1	91.9	99.9
Winter	Crawlers.....	4,000*	1,063	26.5	73.5	73.5
	Settler crawlers to second instar.....	1,063	334	31.4	68.6	91.6
	Second instar to third instar.....	334	45	13.4	86.6	98.8
	Third instar to egg sac.....	45	5	11.1	88.9	99.8
Spring	Crawlers.....	4,000*	1,456	36.4	63.6	63.6
	Settled crawlers to second instar.....	1,456	374	25.6	74.4	90.6
	Second instar to third instar.....	374	35	9.3	90.7	99.1
	Third instar to egg sac.....	85	4	11.4	88.6	99.9

* Estimated number. An average of 200 crawlers per female, 20 females observed each season.

the beetles dispersed, and a relatively large proportion of survivors from third instars (24.1 per cent) were able to produce egg sacs in the summer. However, this is only 0.37 per cent of the 1,894 originally settled crawlers, which represents 99.63 per cent mortality after crawler settling.

A similar pattern of mortality occurred in the other seasons, with a very high proportion of scales destroyed by *vedalia* and *Cryptochaetum*, and the survival of a very low percentage of individuals that leave progeny.

Absolute mortality is high in the younger stages. Per cent mortality,

however, reaches the highest figures in the second and third instars and reaches a cumulative figure of 99 per cent by the third instar. Note that the effects of physical factors on the stages where mortality causes were definitely determined were negligible as compared to the effects on mortality of the two biotic factors: *vedalia* and *Cryptochaetum*.

Limitations imposed by time and travel made it impractical to study the fate of colonies of scales in regions other than Riverside. However, observations and other studies indicate that the patterns of survival and mortality are similar in the coast and the desert.

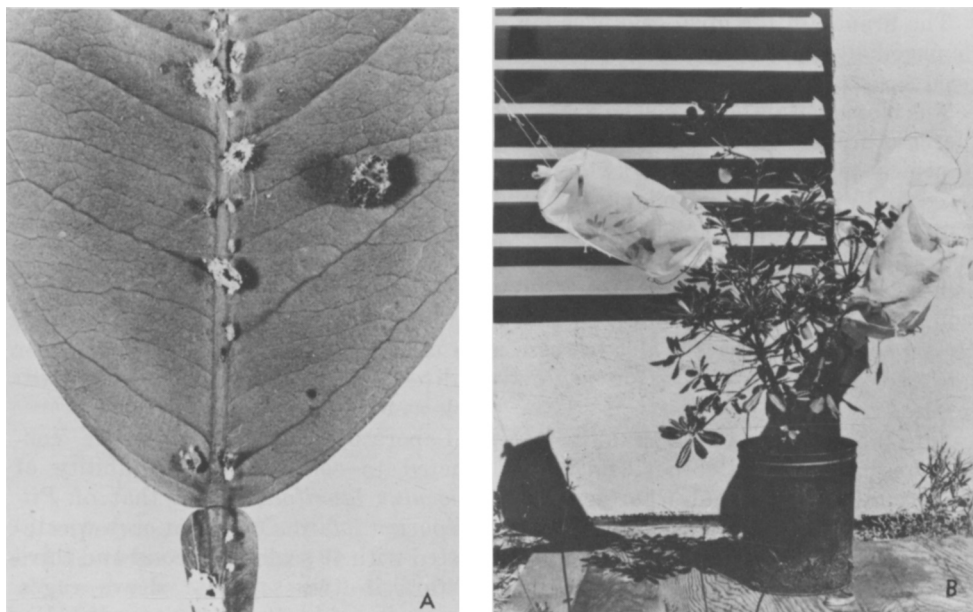


Fig. 11. A: Discriminatory predation of *I. purchasi* by vedalia. The scales containing mature larvae and/or pupae of *C. iceryae* were "spared" by the beetle. B: *Pittosporum tobira* plant infested with *I. purchasi*, with branches covered with sleeves, as used to determine the stages of *C. iceryae* that are not destroyed by vedalia.

EXPERIMENTAL STUDIES WITH POPULATION REGULATIONS

Sleeve cage experiment

A sleeve cage experiment to test the effectiveness of *Cryptochaetum* was set up in Rancho Santa Fe, in the coastal region, January, 1968. The fly had been found to be dominant over vedalia during the winter and early spring, as indicated by life table studies of *Icerya purchasi* in that region. A Valencia orange tree was selected and two of its branches were infested with approximately 200 scale crawlers each. Both branches were covered with sleeve cages of the type used by Smith and DeBach (1942) and DeBach, Dietrick, and Fleschner (1949). About one month later, colonies of the scales were well established on both branches. One of the sleeve cages was opened to expose the scale colony to the action of its natural enemies; the second sleeve cage was left closed. At this time, the weather was cold, but *Cryptochaetum* was seen flying

in the orchard. Forty days after the sleeve cage was opened, there were evident signs of parasite attack in about 48 per cent of the scales. At the middle of April, two months after the cage was opened, *Cryptochaetum* were seen emerging, and almost all the scales on the branch were dead, 95 per cent of them due to the attack of the fly. Only two of the scales appeared to have been killed by vedalia, which was occasionally seen after early April. The experiment is herewith summarized:

Condition of scales:	Open sleeve	Closed sleeve
	Per cent	
Parasitized by		
<i>C. iceryae</i>	95	0
Killed by vedalia	2	0
Dead, unknown causes.	2	—
Lost	1	—
Alive	0	95±

The branch in the open cage was not damaged by the scales and eventually produced fruit.

The closed sleeve cage showed a great increase in scale infestation, the adults of which began producing crawlers by the middle of April. Honeydew and sooty mold were accumulating by the end of May. In July, the branch was completely killed by the scale infestation. This is experimental proof that *Cryptochaetum* by itself is able to regulate the cottony-cushion scale at low levels.

Life table studies of the scale in this same orchard showed 85 per cent parasitization by the fly and 3 per cent destruction by vedalia in the winter. Figures of 91 per cent parasitization and 4 per cent predation were recorded in the spring (table 8). This corresponds very closely with the results of the sleeve cage experiment, and supports the proof that *Cryptochaetum* is capable of controlling the cottony-cushion scale at low population levels in certain areas of the scale range of distribution, and under certain climatic conditions.

Host-plant effects on natural enemies of scale

Bodenheimer (1951) found that vedalia adults and larvae eat fewer scales and have a longer life cycle when it is on Scotch broom, *Spartium junceum*, than when it is on citrus. He also regarded *Pittosporum tobira* as an optimum host plant in relation to vedalia. Host-plant-induced effects could be important in interpreting some of the interactions of the competing natural enemies of the scale, as well as their efficacy.

To clarify these effects, we took samples in the field from naturally occurring infestations, or from purposely infested host plants. They helped to show the relative suitability of certain plants for the development of the scale, as well

as for the performance of its natural enemies. *Pittosporum tobira*, for example, is an excellent food plant for the scale and its enemies. All three species can do very well on it. *Coccus laurifolius* may support large colonies of the scale *Icerya*, but although *Cryptochaetum* was found repeatedly, vedalia never was. This suggested a differential effect of this host plant on the two natural enemies, acting either directly as an unsuitable habitat for the beetle, or indirectly by making the scales unsuitable as food for it.

Laboratory experiments were conducted to compare the suitability of *Coccus laurifolius* with that of *Pittosporum tobira*. One plant each was infested with 40 scales of second and third instars in two separate sleeve cages. Two pairs of beetles were introduced in each of the sleeve cages. The beetles on the *P. tobira* plant fed and oviposited normally, their larvae developing so well that more scales had to be supplied after 12 days. The adults lived from 31 to 42 days. When the experiment was discontinued, all 86 available scales had been consumed. The beetles with *C. laurifolius* did not feed during the first four days and mostly remained off the plant on the sides of the cages. Hunger finally forced them to eat, but only a few scales were taken. The beetles, looking weak and sluggish, lived only up to 15 days. Two eggs were deposited, but no further development was observed. In a second test, the results were similar. Normal breeding took place in the *P. tobira* cage, whereas in the *C. laurifolius* cage, even though one of the beetles lived 23 days, only three eggs were deposited and no progeny was obtained.

A third experiment was conducted to learn if larvae of vedalia would feed and develop on scales on *Coccus laurifolius*. Again the results were negative. The larvae lived only four days and did not feed. The larvae on the

TABLE 12
POPULATIONS AND ACTIVITIES OF *Icerya purchasi* AND ITS NATURAL ENEMIES
FOR SIX WEEKS AS AFFECTED BY DIFFERENT INFESTED AND
POTTED HOST PLANTS LEFT NEAR U.C.R. INSECTARY

Host plant	Approx. no. of scales	Vedalia*			No. scales with <i>C. iceryae</i> exit holes
		Feeding	Egg laying	No. adults obtained	
<i>Citrus aurantium</i>	100	N	N	18	16
<i>Pittosporum tobira</i>	400	N	N	26	47
<i>Cocculus laurifolius</i>	100	P	P	2	67
<i>Spartium junceum</i>	100	LN	LN	6	32
<i>Cassia artemisoides</i>	100	N	N	15	24
<i>Nandina domestica</i>	100	N	N	9	21
<i>Acer oblongum</i>	100	LN	LN	4	18

* N = normal; LN = less than normal; P = poor.

Pittosporum tobira plant fed normally and developed to adults.

In order to test the suitability of *C. laurifolius* and other plants to natural enemies under field conditions, a series of different species of potted plants infested with all stages of *I. purchasi* were left in the open near the University of California Riverside insectary. They were visited by vedalia and *Cryptochaetum* the next day. However, while all plants were equally attractive to the fly, vedalia was active on all but *C. laurifolius*, which was only occasionally visited by the beetles. After about two weeks, when the scales were reduced to scarcity on the other plants, some vedalia stayed on the *C. laurifolius* plant for longer periods of time, and even laid eggs, although in relatively smaller numbers. Eggs hatched in this case, and the larvae fed on the scales but with an evident declining voracity as compared to larvae on other plants. Complete development, however, occurred on *C. laurifolius* in this instance, but the number of adults obtained was small. Table 12 shows the results of this experiment. The difference between this and the laboratory tests may have resulted from vedalia adults feeding on scales of other plants before laying eggs on *C. laurifolius*. *Spartium junceum*

and *Acer oblongum* also were distinctly less suitable for vedalia.

During the summer and fall, 1968, there was an unusual opportunity to study this phenomenon in nature. Two large *Cocculus laurifolius* plants were found heavily infested with the scale in the gardens of a hotel in Soboba Springs, California. When the observations were begun, it was apparent that most of the scales had been attacked in the spring by *Cryptochaetum*, but still enough crawlers had been produced to result in an increase of the population. Previous evidence of vedalia was very slight. Fortunately, there was a fairly large *Pittosporum tobira* nearby, also infested by the scale, although at a lower density than the *Cocculus* plants. Other nearby host plants, such as *Nandina domestica* and English ivy, *Hedera helix*, were also infested, which permitted comparative observations. The number of scales on all but the *C. laurifolius* plants were counted, and frequent visits to the site were made in order to make counts. The population of *C. laurifolius* was estimated because of the very high density. Samples were taken from the *Cocculus* plants at each visit and brought to the laboratory to record accurately the presence of eggs or larvae of vedalia, which may be diffi-

TABLE 13
POPULATIONS AND ACTIVITIES OF *Icerya purchasi* AND ITS NATURAL ENEMIES
AS AFFECTED BY FOUR INFECTED HOST PLANTS FOUND IN A
HOTEL GARDEN IN SOBOBA SPRINGS, CALIFORNIA.
MID-JULY, 1968, TO FEBRUARY, 1969

Host plant	Approx. no. scales	Vedalia*				No. scales with <i>C. iceryae</i> exit holes
		Visiting	Feeding	Egg laying	No. adults obtained	
<i>Pittosporum tobira</i>	526	N	N	N	28	31
<i>Nandina domestica</i>	121	N	N	N	14	17
<i>Hedira helix</i>	137	N	N	N	9	11
<i>Cocculus laurifolius</i>	<20,000	P	P	P	3	<50,000

* N = normal; P = poor.

cult to do in the field in such a dense population. The observations were started in mid-July, 1968, and completed in February, 1969. It became evident at once during the summer that vedalia very rarely attacked the scales on *C. laurifolius*, while it regularly did so on the other three plants (table 13).

Table 13 shows that vedalia, although present when observations were started in July, only rarely attacked the scales on *Cocculus laurifolius* even though a very large population was present. The small number of adults that developed on that plant did so late in the summer, after the scales on the other plants were depleted. Adults were seen visiting the *C. laurifolius* only twice—again, at the end of the summer. *Cryptochaetum* developed on all the plants, especially later in the summer, and was the only one reared from samples taken from the *C. laurifolius* plants, until the few vedalia adults finally issued. This phenomenon is not ascribed to a “monopoly” of *Cryptochaetum*, which may occur when the fly finds a colony of the scale before vedalia does. In fact, *C. iceryae* began to recover in large numbers only very late in the summer, so that they could not possibly monopolize the tremendous numbers of scales on *C. laurifolius*. Besides, their particular mode of development permits many scales to produce crawlers, despite their

being parasitized. A new brood of scales began to develop at the end of the summer, so food was abundant for the beetles which were issuing nearby on the more suitable plants. However, as shown by the data in table 13, their attack on the scales on *C. laurifolius* was negligible. The scales continued to develop during the fall and gradually yielded more and more *Cryptochaetum*. By late winter (February, 1969), the scale had been brought under control by the fly.

It is noteworthy that during the same period (summer, 1968) this phenomenon was being observed in the Soboba Springs Hotel garden; vedalia was also very active in nearby San Jacinto on *Pittosporum tobira* bushes and in a grapefruit orchard in Hemet. In this orchard, the scale population was upset by a methyl-parathion spray applied early in 1968. Some adult beetles were released in August. They quickly became established and began bringing the scale under control by the end of the year.

It is fairly well established, therefore, that *I. purchasi*, when developing on *Cocculus laurifolius*, is almost immune to the attack of vedalia. Other plants seem to have similar effects, such as *Acer oblongum* (table 12), *Spartium junceum* (table 12; Bodenheimer, 1951; Priore, 1963), and gorse, *Ulex euro-*

paeus (V. P. Rao, personal communication). The literature gives some indications of the apparent deterrent effect exerted by these plants, or by the scales raised on them, on the vedalia beetle.

Ulex europaeus, *Spartium junceum*, and *Genista aethneuris*, all Leguminosae, contain several alkaloids (Henry, 1939; Trier, 1943) that may be responsible for immunity they appear to have for vedalia, as shown by Poutiers (1930). *Cocculus laurifolius*, as well as other Menispermaceae, also contains several alkaloids (Henry, 1939; Trier, 1943), that, although different from those of the Leguminosae, may also prevent vedalia from reproducing on this plant.

The experiments and observations reported here also demonstrate that *Cryptochaetum*, acting alone, is able to bring the scale under control, not only in the coastal regions, but also in the interior, when the beetle is handicapped for some reason. Plants such as *Cocculus laurifolius* may have good potential in the experimental evaluation of the effects of natural enemies in host-population regulation, as is done with the insecticidal check method (DeBach, 1946, 1955) and the sleeve cage method (Smith and DeBach, 1942; DeBach, Dietrick and Fleschner, 1949). It permits another type of exclusion test involving comparison of host population trends in the presence and absence of particular natural enemies.

Ant effects

The influence of ants upon the efficiency of natural enemies in prey population regulation has been studied by several workers (Flanders, 1943, 1945, 1951, 1958; DeBach, Fleschner, and Dietrick, 1951; Banks, 1958; Steyn, 1958; and others) and has been reviewed by Way (1963). Some ant species have been found to afford protection to scale insects from the attack of

their natural enemies. Thorpe (1930) stated that the Argentine ant, *Iridomyrmex humilis* Mayr, and the ant *Solenopsis* interfere with *Cryptochaetum* oviposition while not disturbing vedalia at all. Bartlett (1961) observed that *I. humilis* was aggressive to the adult beetles, disturbing them, while the larvae were not attacked. Reports of species of ants attending and protecting *I. purchasi* colonies have been given by Silvestri (1930) and Bodenheimer (1930), the first author ascribing the protective role to *Polyrhachis dives* F. Smith, and the second to *Camponotus compressus thoracica* Wheeler.

A series of observations were made on the effect of several species of ants on vedalia and *Cryptochaetum* and on their ability to control *I. purchasi* in southern California.

Field experiment.—A young lemon orchard in Rancho California, Temecula, provided a good site for an experiment to test the effect of two species of ants on the effectiveness of the natural enemies of the scale. A young isolated lemon orchard in Rancho California, Temecula, was well infested with two species of ants: *Myrmecocystus mimicus* Wheeler, a large brown species and the most abundant, and *Solenopsis xyloni* McCook, a small, light-brown species. Twenty trees were selected in the orchard, all having ant-tended scale colonies developing on them. Ants were eliminated from ten of the trees by applying tanglefoot around their trunks. Their lower branches were pruned to eliminate any chance for the ants to crawl up those touching the ground. The other 10 trees were left as they were to permit normal activities of the ants. The number of scales in every tree was counted at the beginning of the experiment, July 15, 1968, when the ants were reaching peak activity, and were counted when they reached their maximum densities two months later,

TABLE 14

EFFECTS OF *Myrmecocystus mimicus* AND *Solenopsis xyloni* ON SCALE CONTROL BY *Cryptochaetum iceryae* AND *Rodolia cardinalis* IN A LEMON ORCHARD, RANCHO CALIFORNIA, TEMECULA, SUMMER-FALL, 1968

Tree condition	Replicate no.	Scales initially	Max. scale density	Relative max. increase	Time req. to control*	Natural enemies			
						Vedalia		<i>Cryptochaetum</i>	
						Adults	Scale mortality	Scale with exit holes	Scale mortality
With ants:	1	45	156	246	89	28	96.1	3	1.4
	2	48	172	258	103	23	94.0	7	4.0
	3	60	180	200	89	15	96.9	2	1.1
	4	80	186	132	103	14	88.4	18	9.6
	5	85	203	138	81	32	87.7	21	10.3
Average		63.6	179.4	194.8	93	22.4	92.7	10.2	5.3
Without ants:	1	47	100	112	76	14	85.0	13	13.0
	2	49	85	73	76	31	98.0	0	0.0
	3	60	86	43	81	22	84.1	12	13.9
	4	78	150	92	81	30	94.0	6	4.0
	5	85	100	17	76	9	70.0	23	28.0
Average		63.8	104.2	67.4	78	21.2	86.3	11.1	11.7

* In every case, number of days between first time natural enemies seen and the time at which a tree showed an almost total destruction of scales.

at which time ant activity was much greater. Five trees in each category were found to have very similar initial scale densities. Only these are compared in order to avoid density differences influencing the result. From these data (table 14), the following conclusions were drawn:

1. Average maximum densities attained by the scale colonies in those trees having ants were much greater than the densities attained by colonies on ant-free trees.

2. The number of vedalia adults that developed from each scale colony was almost the same in both situations; that is, beetle reproduction was not hindered. Although at times interfering with the activities of adult vedalia, the ants seem to ignore, and even avoid, the larvae, whose defense secretions repel the ants quickly. Similar behavior of the more aggressive Argentine ant, *Iridomyrmex humilis*, was reported by Bartlett (1961), and confirmed in one of our observations, the details of which are given later.

3. The number of scales parasitized by *Cryptochaetum* in either situation was not significantly different. This may indicate that the ants did not interfere too strongly with the fly. The rapid mode of oviposition of *Cryptochaetum* may have permitted successful reproduction in the ant-attended colonies as it did in the ant-free ones.

4. The average time needed by the natural enemies to destroy the scale colonies (78 days) was shorter in those trees from which the ants were eliminated. In ant-tended trees, natural enemies required an average of 93 days (20 per cent longer) to control scales. This was an indication of interference by ants with the oviposition and/or feeding of the predators and parasites.

There was no apparent difference in the degree of interference with particular natural enemies exerted by the two species of ants tested.

Thus, on the basis of comparable initial densities there seems to be little or no difference in effects of these ant species on *Cryptochaetum* as compared to vedalia. Each natural enemy uses its own behavioral devices to minimize such interference and succeed in reproducing.

In both cases, the natural enemies were able to inflict approximately 98 per cent mortality. But, as shown by H. S. Smith (Huffaker and Messenger, 1964), and emphasized by DeBach (1965), the population density at which regulation occurs is not determined by total per cent mortality but by the rate at which mortality increases with density. The effectiveness of vedalia and *Cryptochaetum* was interfered with by ants, so that the rate of mortality of the host was slowed. The scale was then able to attain higher population densities in the trees with ants than on those without them. Control of the scale was attained in both cases, but the maximum densities attained were different, averaging 104.2 on the ant-free trees and 174.9 on the trees with ants.

Cage experiment. One of the "competition cages" described in Materials and Methods was used to study the effects of ants on the natural enemies and on regulation of the scale. Two *Pittosporum tobira* plants, each infested with about 500 scales of second and third instars, were placed in the outdoor cage with a naturally-occurring ant colony present nearby. One of the plants was placed on a tripod whose legs were smeared with tanglefoot to exclude ants from the plant. The other plant was accessible to the ants. Within a few days after starting the test, the accessible plant was being visited by a large number of Argentine ants, *Iridomyrmex humilis*. At this time, ten vedalia adults and ten *Cryptochaetum* were released into the cage. The beetles were seen to be attacked by the ants,

whose approach was mostly frontal. The beetles reacted by avoiding them, moving around the branches and at times flying to the screens of the cage. Some would simply retract their legs under their bodies, a behavior that usually resulted in the ants desisting from their attack. Oviposition occurred after a few days and the eggs were never seen to be destroyed by the ants. The beetle larvae appeared to feed normally, and the ants did not seem to interfere much with them. In fact, when the ants approached them and touched them with their antennae, the ants were seen to make sudden retreats. Tiny droplets of a presumably defensive secretion were observed to emanate from the pleural areas of the beetles. Because of this, the larvae were left undisturbed most of the time. *Vedalia* pupae were never attacked by the ants. *Vedalia*, as most coccinellids, may have a glandular defense mechanism with secretions, usually quinones, that are repellent to predators and may well be repellent to ants.

Cryptochaetum suffered from more interference by the ants, which readily attacked the flies when they were exploring the scales and trying to oviposit. The flies reacted by quickly flying away and stubbornly returning to another point to explore another scale for oviposition. Some would succeed in their oviposition attempts before the patrolling ants found them and chased them away. This was only possible by the quick mode of oviposition of the fly, which takes only a few seconds, an observation already reported by Thorpe (1930). The aggressiveness of the Argentine ants toward *Cryptochaetum* was remarkable and was not matched by that of any other of the species of ants observed. A fly was seen on one occasion to be suddenly grabbed by an ant and torn into pieces by its captor and other ants that rushed to the spot.

Another fly was seen to be bitten by an ant, then escaping injured, fell to the soil. Several ants descended the plant and quickly destroyed the fly. The aggressiveness of *Iridomyrmex humilis* toward *Cryptochaetum* went even further. It attacked the pupae within the scale bodies. The ants would chew through the scale integument, then through the fly puparium and gradually empty its contents. This was observed to occur in at least 12 parasitized scales. The ants were never observed chewing healthy scales. It is noteworthy that when an adult *Cryptochaetum* was smeared with the blood of a *vedalia* larva, it repelled the ants for at least ten minutes, after which it was grabbed by some of them and killed.

On the ant-free plant the activities of the natural enemies were normal. While more *Cryptochaetum* were seen exploring the scales on this plant, there was no apparent difference in the activity of *vedalia* on the two plants. This experiment lasted 48 days. Results are shown in table 15.

The figures presented in table 15 indicate that the effect of *Iridomyrmex humilis* is more drastic on *Cryptochaetum* than it is on *vedalia*. The figures obtained from the ant-free plant are similar to those which have been obtained in competition experiments (both enemies released at the same time). The presence of ants differentially favored *vedalia* by more seriously interfering with its competitor.

Field observations. When inspecting tagged scales or colonies for life table or census studies, attention was paid to the presence of ants to detect any possible effect on the natural enemies. Moreover, whenever colonies of the scales were sampled, the presence of ants was recorded, and specimens collected and identified. Five species of ants were observed during three seasons on eight different host plants and

TABLE 15
EFFECT OF NATURALLY OCCURRING *Iridomyrmex humilis* ON VEDALIA AND
Cryptochaetum COLONIZED ON TWO SCALE-INFESTED *Pittosporum tobira*
PLANTS IN COMPETITION CAGES, RIVERSIDE, SUMMER, 1968

Plant condition	Time req. for scale control*	Vedalia produced		<i>Cryptochaetum</i> produced
		Adults	Larvae	
	Days	Number	Number	Number
Without ants.....	33	51	17	32
With ants.....	47	61	22	13

* Number of days between release of natural enemies and almost complete destruction of scales.

in 12 localities scattered in the three test regions of southern California. In all observations, the final outcome was that eventually the scale colonies were reduced to very low numbers, but in most of them an interim protection seemed to be derived from the presence of ants. Species of ants observed were: *Iridomyrmex humilis*, *I. analis* Andre, *Myrmecocystus mimicus*, *Solenopsis xyloni*, and *Solenopsis* sp. Of these, *I. humilis* was most widely distributed, was found on more host plants, and was the most aggressive of all. The aggressiveness of the other ants was inversely related to the order in which they are listed above.

It should be pointed out that in several instances, heavy colonies of *Icerya purchasi* on *Pittosporum tobira* could not be related to the presence of ants, but heavy spider webbing and accumulated debris which is characteristic of this plant may protect the scale from its natural enemies. Heavy colonies found on citrus, ivy, acacia, and others, were nearly always attended by ants.

Discussion. Survey and periodic census data cast light on the distribution and abundance of the host and natural enemies, and indicated that the scale is maintained at low population levels by the action of its enemies throughout its range. Life table studies gave strong evidence (table 6) but not absolute proof of scale control by vedalia and *Cryptochaetum*. The real proof of regulation of the host by its enemies was obtained from experimental tests (tables 7, 8 and 9).

Under natural conditions, the cottony-cushion scale has a tremendous potential for increase, which is evident when insecticide-induced upsets occur. However, its two natural enemies inflict such a high mortality rate (table 11) that total mortality practically equals natality—for only a very small fraction (.01 to 0.2 per cent) of the crawlers with which the population started survive to leave progeny.

Factors adverse to control, such as ants or climate, are not sufficient to reduce the effects on cottony-cushion scale of its natural enemies.

EFFECTS OF COMPETITION BETWEEN *Rodolia cardinalis* AND *Cryptochaetum iceryae*

According to the competitive displacement theory (DeBach and Sundby, 1963; DeBach, 1966), vedalia and *Cryptochaetum*, which have a common niche requisite—food (*I. purchasi*)—can be

said to be ecological homologues. Thus, it would be expected that their competition for the cottony-cushion scale should result in the displacement of one enemy by the other, which does in-

deed occur in the desert, where *vedalia* is dominant and on the coast where the fly is dominant. In the interior, however, their competitive abilities appear to be fairly evenly balanced. If *vedalia* and *Cryptochaetum* are considered to be ecological homologues, their apparent coexistence would be contrary to the competitive displacement principle.

The main objectives of the studies herewith described were to determine if interspecific competition between natural enemies (a) has any effect on the population regulation of the prey, and (b) if it results in displacement of one enemy by the other, or rather, whether true coexistence of the two may occur.

The first objective bears on the biological control policy practice of introducing more than one natural enemy, the desirability of which has been challenged by Turnbull and Chant (1961). These authors assume that the competition of two or more natural enemies for the same host would be advantageous for the host, whose populations would be enhanced rather than suppressed as a result of such competition. Watt (1965) and Turnbull (1967) have also challenged multiple introduction of natural enemies as a biological control practice.

The second objective (to establish "coexistence") was of both theoretical and practical interest. Competitive displacement between ecological homologues has been rarely observed in nature (DeBach and Sundby, 1963), and this could be an opportunity to record its occurrence in the case of *vedalia* and *Cryptochaetum*. We could also further test the soundness of importing of multiple natural enemies for biological control purposes. Competition between natural enemies, as postulated by the competitive displacement principle (DeBach and Sundby, 1963; DeBach, 1966) normally is not detrimental to host population regulation. The displacement of an effective entomophagous species by

another species means that the second is more effective and will therefore produce better host population regulation.

Distribution and abundance of *vedalia* and *Cryptochaetum*

Displacement of *Cryptochaetum* by *vedalia* tends to occur in the desert and is only prevented by the annual immigration of *Cryptochaetum* during the winter. The reverse occurs on the coast, where the beetle tends to be displaced by the fly. The outcome of competition between the two species is indirectly influenced by climate through its effect on their relative rates of increase. In the interior, both enemies are common and overlap in their distribution, because their competitive abilities are apparently nearly evenly balanced. However, the prey is shared in differing proportions depending on the prevailing environmental conditions.

Most observers with whom we had talked about this problem originally believed that in the interior, *vedalia* would overwhelm the scale colonies and destroy them indiscriminately, including the immature stages of *Cryptochaetum* that might be present in the parasitized scales. This should have produced a relatively rapid competitive displacement of the fly by *vedalia* in the interior area a long time ago. However, such displacement has not occurred in 80 years—unless the process is masked, because both species disperse into the interior from their respective areas of dominance in the desert and on the coast. The two natural enemies have the same, and only one, food source—*I. purchasi*. Thus they can be considered to be ecological homologues (DeBach and Sundby, 1963). However, the two natural enemies appear to coexist in the interior region.

Early survey data obtained in August, 1967, indicated that *Cryptochaetum* had been active in certain scale colonies in Riverside since at least July

of the same year. This was contrary to common belief, for the parasitic fly was thought more likely to be found here during the fall and winter. Of even more interest were the colonies that yielded *Cryptochaetum* in large numbers and did not show any evidence of vedalia attack, even though the beetle was active during the same period on other plants nearby. The vedalia did not appear in the aforementioned colonies until two or three months had passed. One would then expect them to increase greatly in numbers as usually happens when they take over other colonies. Although the scales were gradually reduced to low population levels by both enemies, the numbers of the beetle recovered from these colonies were not especially large. Thus, it was apparent that in this area vedalia was not the major regulator of scale populations, and that significant interactions between the two enemy species must occur in the interior. It is noteworthy that the plants on which these colonies were established, as far as was known, had never been sprayed or otherwise disturbed, except for some pruning in the previous spring. They also were free of ant colonies that may affect the efficiency of enemies. The survey thus indicated that the time at which one enemy finds a colony may be an important factor in the outcome of competition in that particular spot.

The following series of experiments were designed to test the hypothesis (based on observations) that under natural conditions vedalia will not attack parasitized scales in which certain stages of the fly, probably the more mature ones, are present.

At this time, a field test was being made in the Biological Control Grove. One of the tagged scales used in life table studies had produced a colony of 37 young scales which had settled on a small branch having nine leaves. A sketch of the branch was made, and the

scales were marked with a number in the sketch. Some of the scales showed signs of having been parasitized, and, in fact, one fly was seen emerging from one of them after a few days. A recently formed vedalia pupa was observed on one of the nine leaves. When this pupa emerged, the adult began feeding on some of the scales and remained in the colony for four days. The scales, with evident signs of parasitization were not touched by the beetle (fig. 11A). Two more beetles, which fed on some of the scales, were observed on these leaves later. Scales were observed as follows:

Unparasitized, taken by vedalia.	13
Parasitized, taken by vedalia...	0
Parasitized that yielded	
<i>C. iceryae</i>	18
Escaped attack.....	2
Dead by unknown causes.....	1
Lost	3
Total	37

A similar observation was made in Loma Linda, Riverside County, on a colony of 28 immature scales established on a *Cassia* sp. plant.

In the course of life table studies of *I. purchasi*, scales that were parasitized by *C. iceryae* were repeatedly observed to be left untouched by vedalia. In periods of host scarcity, the vedalia were seen to chew on such scales, leaving the fly pupae intact, attached to the scale remains. In all instances observed, the fly successfully emerged from such exposed pupae. In three instances, one beetle was seen feeding inside a scale egg sac for two or three days. Most of the eggs were eaten; but the scale body, which contained *C. icerya* pupae, was left intact. When observing the scales from samples taken from different regions, this "sparing" of parasitized scales was again evident.

An experiment was designed to determine the exact stage or stages of *Cryptochaetum* that are immune to vedalia destruction. A *Pittosporum tobira*

plant infested with approximately 400 scales of second and third stages was obtained. Small organdy sleeves were used to enclose four branches, while the rest were left uncovered, as shown in fig. 11B. The plant was confined in a "competition cage," and 20 *Cryptochaetum* were released into it. The flies were allowed to oviposit in the uncaged scales until they died four days later. Five days later, one of the sleeves was removed, and another 20 flies were liberated. The three other sleeves were removed at intervals of five days, and 20 flies were released each time. In this way, after 24 days, all immature stages of the fly, from egg to pupae, were represented on this single plant. This was ascertained by dissecting 10 scales from each branch.

Twenty vedalia were then released and their activities observed every day. The beetles fed, mated, and oviposited on all branches, and soon their larvae began to feed on the scales. Ten days after vedalia was introduced, and 34 days after the experiment was started, *Cryptochaetum* began to emerge and kept emerging for the next 11 days. A total of 62 flies emerged. They came from the scales on the uncaged branches and the branch whose sleeve was removed first. These corresponded to scales which contained pupae and mature larvae of the fly, respectively, at the time at which the beetles were released. On these branches, the parasitized scales were clearly spared by the beetles and their larvae, in contrast with the total destruction of the scales, including those containing young *Cryptochaetum* larvae, on the other branches.

This discriminatory predation on the part of the vedalia may be another evidence of its high specificity, and is contrary to what Koebele (1890) concluded from his observations in Australia and Hale's (1970) in Hawaii. It also contradicts the belief that coccinellids in general indiscriminately at-

tack healthy and parasitized scales, as stated by Berlese (cited by Howard, 1930).

Competition experiments

Based on these tests and observations, experiments were conducted to expose the scale to the attack of its two enemies in three different situations corresponding to three hypothetical circumstances in which the vedalia and the fly may compete: (a) the colony of scales is first found by the fly, later by vedalia; (b) it is first found by the beetle, later by the fly; (c) both enemies find it at about the same time. (In situations (a) and (b), sufficient time had to elapse for the first species to be well established before the other arrives.)

The tests were conducted in the field at U.C. Riverside in competition cages which were large enough (112 ft²) to permit apparently normal behavior by the parasitic fly. The large cages also allowed the experimenter to enter the cages to make close-up observations and counts, as well as to introduce new or remove old infested plants as necessary. Temperature conditions were found to be essentially equal inside and outside the cages. In all the experiments, a *Pittosporum tobira* plant infested with about 500 scales of second and third stages was used in each cage. Ten vedalia and 10 *Cryptochaetum*, five pairs of each, were released in each cage. The number of natural enemies that developed was carefully counted in each cage with vedalia adults and larvae recorded separately. By using three cages at one time, it was possible to run all experiments simultaneously and to replicate them in each season of the year. A description of the three types of experiments (as carried out during the summer) follows, in order to illustrate the general events that took place in all seasons.

Experiment 1: *Cryptochaetum* released first. Test releases of the para-

sites had shown that flies liberated late in the morning or in the afternoon tended to gather in the sunny areas of the cage, to fly repeatedly for long periods, and eventually to become exhausted and fall to the ground. The flies, therefore, were released very early in the morning to enable a better adjustment to the conditions of the cage. With this practice, they lived and oviposited for about three or four days, which is approximately normal. Dissections of scales after eight days showed the presence of small parasite larvae; scales dissected 20 days after the release of the parasites showed mature larvae. At this time, the vedalia beetles were liberated in the cage. They began feeding and eggs were laid the next day. One week later, the activity of vedalia larvae was evident and the scales were intensively destroyed. At this time the first *Cryptochaetum* began to emerge and continued to do so every day for nine days. They were captured beginning two days after the start of emergence, at intervals of two days, and their numbers recorded. The first vedalia adults did not emerge until 18 days after their parents were released. Only small groups of scales were left at this time, 38 days after the parasite release. Some larvae and adults of vedalia were seen wandering on the plant, the bench, and the screen of the cage, a typical behavior in the face of food scarcity. Even cannibalism was observed to take place under these conditions, the adults and larger larvae feeding on small larvae and pupae. It was at this peak of vedalia activity that fly emergence was taking place, a fact that strongly confirmed our earlier findings that even starving adults and larvae of vedalia find older parasitized scales unsuitable as food and "spare" them. At the end of this experiment only a very few scales survived. The total *Cryptochaetum* recorded was 207;

the adult vedalia, 51; and the total vedalia larvae that did not reach the adult stage because of scale scarcity was 72.

Experiment 2: Vedalia released first.

Five pairs of vedalia were released in the cage at the beginning of the test. Eight days later, when larval activity was considerable, five pairs of *Cryptochaetum* were released. Soon they were seen ovipositing very actively. Most of the flies lived three days; only two were seen alive on the fourth day. Nineteen days after the experiment was started, F₁ vedalia adults emerged and began feeding, mating, and ovipositing. By the thirty-first day, the activity of adults and larvae had been so intense that only a few small groups of scales were left. Among these scales, several were recognized as being parasitized by *Cryptochaetum*, which then began to emerge in small numbers and kept emerging for four more days. By the thirty-sixth day, almost no scales were left; all flies had emerged, so the experiment was terminated. The progeny counts were: *Cryptochaetum*, 43; vedalia adults, 87; vedalia larvae, 20.

Experiment 3: Both enemies released at the same time.

In this experiment, five pairs each of vedalia and *Cryptochaetum* were released into the cage at the same time. Mating and oviposition activity was normal. Vedalia larvae were abundant after nine days, and the first adults emerged 17 days after the introduction of their parents. This generation, in turn, produced a large number of larvae, some of which reached the pupal stage before the host was depleted. Emergence of F₁ *Cryptochaetum* adults occurred when the second group of vedalia larvae were at the peak of activity. The experiment lasted 36 days, and the results were: *Cryptochaetum*, 49; vedalia adults, 69; vedalia larvae, 26. In this case, the ratio between *Cryptochaetum* and vedalia was

TABLE 16
EFFECTS OF COMPETITION AS MEASURED BY TOTAL PROGENY PRODUCED BY FIVE PAIRS EACH OF *Cryptochaetum iceryae* AND *Rodolia cardinalis* RELEASED IN DIFFERENT SEQUENCES ON ABOUT 500 *Icerya purchasi* (SECOND AND THIRD INSTARS) IN THE SAME CAGE AND REPEATED IN FOUR DIFFERENT SEASONS IN THE INTERIOR, RIVERSIDE, 1967-1968

Experiment number and sequence of release	Total number of progeny											
	Summer (June-Sept.)			Fall (Sept.-Dec.)			Winter (Dec.-Mar.)			Spring (Mar.-June)		
	<i>C. iceryae</i>	Vedalia		<i>C. iceryae</i>	Vedalia		<i>C. iceryae</i>	Vedalia		<i>C. iceryae</i>	Vedalia	
		Adult	Larv.		Adult	Larv.		Adult	Larv.			
1. <i>C. iceryae</i> released first vedalia two weeks later.....	207	51	72	198	27	59	226	38	73	294	64	92
2. Vedalia released first, <i>C. iceryae</i> two weeks later.....	43	87	20	37	68	31	42	83	51	55	66	37
3. Both enemies released at the same time	49	69	26	41	62	37	59	71	28	74	69	42

much closer than in the preceding two tests.

The experiments carried out during the other seasons showed the same pattern of interactions and activities of the natural enemies. In the winter, the development of both was considerably prolonged as compared to the other seasons. The results of all the experiments are summarized in table 16 and figure 12.

Results. Tests showed clearly that when either of the enemies of the cottony-cushion scale finds a colony before the other one does, provided that enough time elapses, that enemy will consume a larger portion of the prey, with a consequent proportionally larger number of F_1 progeny production. Experiment 1 (*Cryptochaetum* released first) favored the fly, since vedalia adults and larvae do not eat scales containing their mature larvae or pupae. Fewer beetles completed development, and more larvae starved without reaching maturity, as compared to Experiments 2 and 3. The numbers of parasites obtained in Experiment 1 in any season were also greater than in the other two experiments. In Experiment 2 (vedalia released first) more vedalia adults than *Cryptochaetum* were always obtained. Moreover, fewer vedalia larvae starved, while fewer parasites were obtained than in Experiments 1 and 3. The flies were not physically inhibited in their oviposition by the vedalia larvae or adults, but their eggs and early larval instars were devoured by the predators along with scale bodies. When both enemies were released at the same time (Experiment 3), the fly appeared to be slightly favored. This advantage may well be greater during the cooler months (winter and early spring), when the life cycle of the beetle can be considerably prolonged, and when its rate of feeding is low (Cressman and Dumble, 1930). This helps explain the field observation

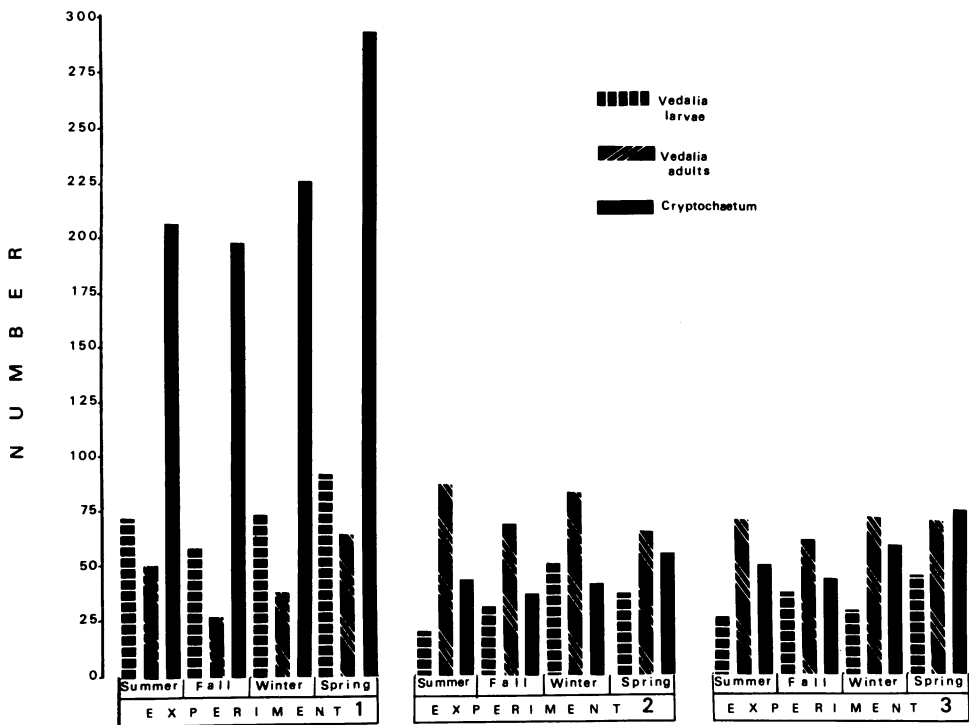


Fig. 12. Competition experiments involving vedalia and *C. iceryae* colonized in the same cage. Experiment 1: *C. iceryae* released first; experiment 2: vedalia released first; experiment 3: both enemies released at the same time.

in the interior when occasionally *Cryptochaetum* "monopolized" scale colonies found on *Pittosporum tobira*, whereas on other occasions, but in the same locality, vedalia took over the scales completely. This shows that in microhabitats weather is not the only parameter influencing the outcome of competition between the two species.

It is evident that the flies, when competing with vedalia, as is common in the interior, can have an initial advantage when finding a scale colony before the beetle does. When the beetle arrives late, it will find many of the scales in the colony already parasitized by mature larval or pupal stages of the fly, which are immune to the attack of vedalia. Only unparasitized scales, the egg sacs, or scales containing early larval stages of the fly will be devoured. This

evidently is the reason why some colonies were observed to keep yielding *Cryptochaetum* alone for a long time, in spite of vedalia being active in the same area.

When vedalia finds the scales before the flies do, they can so nearly destroy the scales that the fly's chances of reproducing (when they arrive) are small. Unless the number of scales is large, or the beetles relatively small in numbers, or the time elapsed between the onset of vedalia attack and the fly's arrival short, the colony may be completely destroyed by vedalia. One colony observed at El Segundo showed an almost complete takeover by the beetle during the summer. At the same time, less than a mile away, *Cryptochaetum* had dominated another colony. Both colonies were established on *Pittospo-*

rum tobira bushes, and neither had ants tending the scales.

When both enemies find a scale colony more or less at the same time, the chances of *Cryptochaetum* reproducing in appreciable numbers are again determined by the density of the colony and the initial number of competing beetles. If the former happens to be large and the latter small, more parasitized scales will remain untouched by vedalia with a resulting larger progeny of the parasite.

From general observations and data, however, vedalia appears to be slightly favored, and it probably has the potential to displace *Cryptochaetum* in the interior. However, the slowing down of the beetle's development during the winter seems to be an advantage to the fly. Moreover, *Cryptochaetum*, being a gregarious internal parasite, which connotes high reproductive capacity, and having a searching capacity apparently as good as that of vedalia, is a formidable competitor. Thorpe (1930) began to visualize these competitive interactions when he wrote:

It is true that *Cryptochaetum* is at a disadvantage in that a large number of larvae may develop in a single host, but it must be remembered that under conditions of plenty the parasite larvae tend to be more thinly spread over the whole infestation. This, however, really works to its advantage when food becomes scarce, since then a relatively small infestation of the *Icerya* will yield a large number of adult flies capable of spreading widely and seeking out isolated colonies of the scale. Under similar conditions but few individuals of vedalia would reach maturity, since each larva requires several hosts in order to complete its development, and the numbers would be so reduced that there would be a serious danger of their being unable to establish themselves on fresh groups of host. It is well known that vedalia is often liable to local extinction in this way, and this difference in life-history of the two insects may be one of the reasons why *Cryptochaetum* is often of great value in searching out and controlling isolated batches of the scale before vedalia has succeeded in discovering them.

Cryptochaetum definitely has competitive advantages over vedalia under certain circumstances. Field observation, rearing data, and competition experiments have shown or strongly indicated that:

(a) The fly may be able to locate isolated colonies of *I. purchasi* more readily than does vedalia.

(b) Scales parasitized by mature larvae and/or pupae of the fly are not eaten by vedalia.

(c) The fly will readily attack scales on *Cocculus laurifolius*, while vedalia virtually will not feed or reproduce on scales on this and certain other plants.

(d) Immature stages of the fly are apparently tolerant to cold temperature.

(e) Scales parasitized after egg sacs are produced generally produce crawlers before they are killed by the parasites, a phenomenon that tends to provide host continuity for the survival of the parasites at very low densities.

(f) The fly is dominant in the coastal areas, from which it probably constantly disperses into the interior area in greater numbers than vedalia disperses from desert areas.

Vedalia, however, competes very effectively with the fly for their common food, the cottony-cushion scale. The beetle is more broadly climatically tolerant and its life cycle is shorter than that of the fly, especially during the summer and fall months. Vedalia is also equally able to find isolated colonies of the scale.

Coexistence experiments

If the two natural enemies are true ecological homologues, their coexistence in the interior would be contrary to the principle of competitive displacement, which states: "different species having identical ecological niches (that is, ecological homologues) cannot coexist for long in the same habitat" (DeBach and Sundby, 1963). A definition of coexis-

tence (DeBach, 1966), expressed as a corollary of the competitive displacement principle, is: "different species which coexist indefinitely in the same habitat must have different ecological niches, that is, they must not be ecological homologues."

If *Cryptochaetum* and the vedalia are considered ecological homologues, coexistence should be only apparent, not real. We consider them as ecological homologues as defined by DeBach and Sundby (1963), for they have an identical food requirement, the cottony-cushion scale. We deduce the reason for their "coexistence" in the interior is that dispersal constantly occurs—the fly from the coast and vedalia from the extreme interior or desert areas. Otherwise, one or the other should be displaced.

Field cage experiments to test the possibility of coexistence in the interior was conducted continuously from June, 1968 through April, 1969. (The experiments were incomplete, hence the results and discussion should be considered accordingly.)

A *Pittosporum tobira* plant infested with about 400 scales of second and third stages was placed inside one of the cages designed for the competition studies described earlier. Then 10 pairs of each of the natural enemies were released simultaneously on June 5, 1968. Additional scales were provided on new host plants as necessary, so that food shortage was not a condition of this experiment.

Summer. Twenty-three days after the test was started, vedalia had completed one generation. The second-generation beetles then began to mate and oviposit, and during their period of larval development, the flies started emerging (July 6). A new plant was provided at this time. The life cycle of vedalia never exceeded 23 days in the summer, during which four generations of the beetle oc-

curred. The number of adults obtained per generation in this season were 18, 26, 32, and 48, respectively. *Cryptochaetum* produced only three generations, with the numbers of adults declining, initially from 19 to 13, and finally to 6.

Fall. Only two generations of vedalia occurred in the fall. The life cycle of the beetle was prolonged from 25 to 57 days as the season advanced. The numbers of adults obtained per generation were 33 and 14, respectively. Many larvae did not complete their development until winter. *Cryptochaetum* also had two generations, with 12 and 21 adults obtained, respectively. The life cycle of the fly did not exceed 33 days.

Winter. Many vedalia larvae were present at the start (December 25) that had not completed their development in the fall. They were mostly young stages. Pupae were not formed until January 18, 1969, and from them, the first adults emerged on February 14. The life cycle of the beetle was prolonged to 86 days during this season. Only one generation occurred, and the number of adults produced was 72. *Cryptochaetum* began emerging at the beginning of January, 1969, the life cycle having taken only 56 days. A second generation of the fly was completed 46 days later, on February 18, when the only winter generation of vedalia had been just completed. The respective numbers of flies obtained were 38 and 51.

Spring. About 30 vedalia larvae that had not completed their development in the winter were initially present. The first generation of beetles occurred in late March, and a total of 22 adults was recorded. Soon they began feeding and reproduction. Early in April, *Cryptochaetum* emerged, and 30 flies were counted in four consecutive days. At this time, however, many vedalia larvae and adults were present in the cage. By the end of April a second generation

of vedalia was completed, and 85 adults were obtained. By May, 1969, when the test was terminated, there was no apparent evidence of *Cryptochaetum*, while the vedalia continued to multiply in the cage.

Results. Vedula clearly overtook the fly during the summer. The life cycle of the beetle was short enough then to allow second generation adults to emerge before any *Cryptochaetum* did. The reproductive capacity of the beetles was also high at this time, so that the total beetle population began to overwhelm that of the fly. The numbers of *Cryptochaetum* became less and less as the summer advanced. In the fall, when temperatures began to decline, and in the winter, when they reached their lowest, the life cycle of vedalia gradually became more and more prolonged and was proportionally greater than that of *Cryptochaetum*. While that of vedalia was more than tripled, the fly's was only doubled at most. This relative difference in the length of the life cycles is an important gear which tends to partially reverse the results of competition between the two natural enemies from summer to winter.

It seems reasonable to conclude that during the summer, vedalia tends to be a strong winner in most of the habitats of the interior region. In the colder months, *Cryptochaetum* tends to win. In the interior, the generally desert-like climate of the summer and fall switches to a somewhat more coastal type during the winter and early spring, thus seasonally reversing the outcome of the competition between vedalia and *Cryptochaetum*. This tends to balance the competition abilities of the two natural enemies and indicates how close the two species are in their overall relative fitness. However, the test results suggest (when the results of spring and summer are combined for a single year) that vedalia should displace *Cryptochaetum*

completely during late spring and summer, more or less after nine generations.

Although delayed in its development by low winter temperatures, a relatively large number of larvae of vedalia overwinter and attain the adult stage early in the spring. As temperatures get warmer, the beetles begin to multiply rapidly, competing with the flies by destroying many hosts as well as the young larval stages of the parasite inside the scale bodies. Thus, successively fewer *Cryptochaetum* attain the older stages immune to vedalia predation. The life cycle of vedalia rapidly shortens by the end of the spring and reaches its shortest in the summer, the time by which, as indicated by these preliminary studies, the beetle may well have displaced *Cryptochaetum*. Thus, we concluded that the "coexistence" of the two natural enemies in the interior is really only apparent, and the practically permanent presence of the two in such areas probably is maintained by migration of *Cryptochaetum* from its area of dominance along the coast.

Two questions arise at this point: First, if all conditions in southern California were of desert type, would *Cryptochaetum* continue to exist? And, second, if all conditions were coastal type, would vedalia continue to exist? The answer to both questions is probably no. If climatic conditions were the same throughout a given area, the winner would be the species that is better adapted to those particular conditions. For example, the successful establishment of *Cryptochaetum* in Chile (González and Rojas, 1966), where it is the key factor in the control of cottony-cushion scale, or the failure of vedalia to get established in the Caspian area of Iran (Kaussari, 1946), are possible illustrations of what would happen if all conditions in southern California were coastal.

Competitive displacement in the interior has not apparently occurred in

California for 80 years, but this does not mean that it is not in the process of occurring or will never occur. The phenomenon has been postulated to take place in nature in a few years to many years (DeBach and Sundby, 1963). Eighty years may not have been long enough for displacement to have occurred in the interior, where they are rather equally balanced competitively. Displacement of the yellow scale, *Aonidiella citrina* (Coquillett) by its ecological homologue, the California red scale, *A. aurantii* (Maskell) in southern California, seems to have required 60 to 70 years (DeBach and Sundby, 1963).

Effect on abundance of cottony-cushion scale

All tests strongly indicate that com-

petition between vedalia and *Cryptochaetum* does not affect biological control of the scale. The beetle and the fly are equally effective singly or in combination, and when for some reason one of them is handicapped in its action, the other one may take over and maintain excellent control of the pest.

The hypothesis of Turnbull and Chant (1961), Watt (1965), and Turnbull (1967), therefore, appears to be strongly refuted: that competition between two or more natural enemies for a single host may be of advantage for the host, whose population would increase as a result of such competition. The refutation of this hypothesis is emphasized here, because of its fundamental importance to the policy of parasite importation for biological control.

DISCUSSION AND CONCLUSIONS

Pemberton and Willard (1918) were probably the first to challenge the value of multiple introduction of parasites for biological control purposes, as discussed by Smith (1929) in his rebuttal of the assumptions of those authors. The argument was revived again by Turnbull and Chant (1961), who were more recently supported by Watt (1965) and Turnbull (1967). Turnbull and Chant, (1961), when expressing their views regarding multiple introduction of parasites, stated: "the proposition that two or more biotic agents attacking a single host may interfere with each other to the advantage of host survival requires amplification."

The study of the mechanisms of competition and coexistence between *Rodolia cardinalis* and *Cryptochaetum iceryae* offered a good opportunity to test the value of multiple parasite introduction, because this predator-host relationship represents an outstanding case of biological control involving two competing natural enemies.

Thorpe (1930) lists seven reasons why vedalia is so successful as an enemy of *I. purchasi*, which we summarize thus: (1) vedalia is largely independent of climatic conditions and is found almost everywhere that the scale occurs; (2) it is a completely specific predator, and each individual attacks and destroys several prey; (3) it attacks all stages of the scale, from egg to adult; (4) it is very active and disperses rapidly, whereas the prey is sedentary; (5) it has, roughly, three generations to one of its prey; (6) it is free from natural enemies; and (7) the scale, due to its large size, cannot easily conceal itself in crevices and is easily reached by vedalia.

According to the same author, *Cryptochaetum* shares all of the above advantages with the exception of (1) and (3). In regard to (1), it has been the common belief that the fly is not found beyond the Riverside region (toward the desert area). We have found, however, that the fly exists all year in Beau-

mont and Banning and is capable of moving at least to Palm Springs during the winter and early spring, and then it disappears from Palm Springs as the weather gets warmer. In the interior the relative fitness of both is nearly equal, but vedalia probably is potentially able to displace *Cryptochaetum*. The coastal areas, however, where the fly is dominant, are refuges from which it probably regularly disperses into the interior. This results in an apparent coexistence of the two natural enemies in this area.

Regarding (3), we agree with Thorpe and would only add that the fly not only restricts its attack to the second, third, and adult stages of the scale, but adults which already have produced egg-sacs when parasitized are almost always able to produce crawlers—depending on the stage of egg-sac development at the time of parasite attack. This fact may bear some importance in the population relations between the host and its enemies. Local extermination of small colonies is generally precluded, because a few hosts usually produce crawlers. This gives a continuity of hosts and enables *Cryptochaetum* to maintain itself in small numbers during the critical host-shortage periods of the year. Some crawler production by scale survivors also occurs with vedalia usually after it has “cleaned-up” a colony and dispersed. This permits the settling of new scales, which may then be found by *Cryptochaetum* before vedalia returns. Often, when vedalia subsequently finds these colonies, the fly already will be present as a competitor. The ability of the beetle to reproduce under these circumstances will depend on: (a) the climatic conditions that will determine its rate of development, and (b) the relative severity of competition from *Cryptochaetum*, which again is influenced by climate.

The dispersal of flies from their coastal refuge would probably be less

important were it not for the subtle mechanism just discussed which results in maintenance of a constant supply of young scales. This speculation may hold true, particularly when the scales occur on *Pittosporum tobira*. This plant provides a protected habitat for the scale and its enemies. At the time when the scale and its natural enemies are very scarce in citrus orchards, isolated colonies of the scale can be found on *P. tobira* bushes, especially those located near buildings. Some of these colonies persist on a plant for long periods of time. One on the U.C. Riverside campus was observed for 18 months. The abundance of scales in such colonies fluctuates from heavy to light infestations, but never seems to be reduced to zero. *Cryptochaetum* has been continuously recovered from several of such colonies, sometimes for up to three months without vedalia being found on them in appreciable numbers. The beetle, however, may be found actively destroying the scale on another *P. tobira* plant, sometimes only a few blocks away. This “monopoly” of a scale colony by either one of the enemies is determined by the one which finds the colony first.

Competition experiments and field observations strongly supported this hypothesis. When the fly finds a scale colony before vedalia does, and its development reaches that of mature larva or pupa, the scales so parasitized will be avoided by vedalia. On the other hand, when the beetle finds the colony first, and its larvae are actively feeding when *Cryptochaetum* comes, the chances for the fly population to develop are reduced. The fly is often able to find isolated colonies before vedalia does, another factor that makes it a good competitor. In the interior during the winter, development time of vedalia increases much more than that of *Cryptochaetum*, enabling the fly to surpass the beetle in the proportion of scales destroyed. In the desert, it moves into

the nearly exclusive domain of vedalia; in the coast, it almost completely displaces its competitor. It is only when the weather gets warmer by late spring that vedalia, whose life cycle then becomes greatly shortened, builds up from small numbers and destroys most of the scales. As the summer advances, the life cycle of the beetle is shortest, and at this time the vedalia is potentially able to displace *Cryptochaetum* in the interior, were it not for the periodic migration of the fly from the coastal zones.

When comparing the properties of *Cryptochaetum* and vedalia, it is found that both usually allow the host population to recover by leaving some few unattacked. One may wonder if this would turn the balance in favor of *Cryptochaetum* under certain circumstances, as when the fly finds a colony before vedalia does. In regard to the effective use of the host, *Cryptochaetum*, as a parasite, seems to have an advantage over vedalia. Theoretically, every egg of the fly will become an adult at the expense of a single scale, usually shared with several other siblings. A larva of the beetle, on the other hand, in most cases, has to feed on several scales in order to attain full development. We agree with Smith (1939) that one larva of vedalia feeding within a large egg-sac of its host can reach maturity, but this occurs only rarely.

Usually more than one egg of vedalia will be laid on a scale, and several larvae will be seen destroying a single scale. Also, if other scales are not available, many of the beetle larvae starve. Cannibalism has been observed in the field—usually the larger larvae eating smaller ones or even prepupae. Cannibalism is probably a necessary adaptation when prey is scarce. This, together with temperature responses in feeding and reproduction, and oviposition responses to prey density, may constitute intrinsic properties that permit vedalia to effectively control its own numbers. Thus,

the beetle has a number of attributes that make it a formidable competitor of *Cryptochaetum*.

If the hypothesis of Turnbull and Chant (1961)—that multiple-parasite competition favors the host—was valid, one would expect to find heavier infestations of the scale in the interior areas of southern California. This has never been observed. It appears that in the 80 years after their introduction into California, the scale's two natural enemies seem to be very similar in their ability to control and are almost perfectly adapted to their environment, each one dominating in one extreme area of the range, and overlapping in the interior area, with excellent control of the host resulting throughout the range.

Turnbull and Chant admit that certain groups of parasites may maintain control by a "division of labor," which might be considered in the case with vedalia and *Cryptochaetum*. The density of the scale in the three regions studied was always similarly low. Density indexes strongly support the view that competition between enemies in the interior area does not result in heavier infestations of the host. The density indexes, which were always low, do not differ much between regions during the same season. Vedalia and *Cryptochaetum* both have proved able to maintain the scale at low population levels. Interspecific competition is primarily responsible for major differences in the distribution and abundance of the two species; climate is only indirectly responsible.

Many studies have been focused on biological control failures; we have studied a successful case of biological control with two competing natural enemies that appear to maintain control indefinitely. Naturally, several questions remain: What is it that repels vedalia from scales parasitized by *Cryptochaetum*? Is it chemical or physical

stimuli? Why are certain host plants, such as *Cocculus laurifolius*, not attractive to vedalia? What is the key to the dispersion of vedalia? How to account for the extraordinary abilities of *Cryptochaetum* and *R. cardinalis* to find isolated colonies of *I. purchasi*? Why does *I. purchasi*, a hermaphroditic species, occasionally produce male scales?

A comparative study of the *Icerya*-natural-enemy complex in Australia as compared to California would be valuable. The region of Australia from which *Icerya* was introduced accidentally (and later, from which its natural enemies were introduced purposely) is located between 30 and 45 degrees south of the equator. California is almost on the same latitude, north of the equator. Both areas have many features in common, with cool coastal areas, mild interior regions, and hot, dry deserts. The fly and the beetle apparently have a similar distribution in California and Australia. Koebele visited the Adelaide area and sent to California stocks of *Cryptochaetum* and vedalia, with the well-known outstanding results.

The senior author cherished an ambition to round off these studies by retracing Koebele's journey in Australia to see the scale and its parasite and predator in their natural surroundings. An opportunity to do this arose in August, 1971, when he attended the Twelfth Pacific Science Congress in Australia. With funds made available by CSIRO, the senior author was able to cover the same ground as Koebele, but by jet instead of train. Like Koebele, he had lit-

tle luck in Sydney and Melbourne, so he proceeded to Adelaide, which Koebele (1890) "considered . . . the best field to obtain the material." Small scattered colonies of the scale were found, showing evidence of *Cryptochaetum* parasitization, just as they do at the corresponding time of the year in California. The presence of an old vedalia pupal skin in one infestation hinted that the activity of this predator may have increased in the previous summer, just as occurs with seasonal changes in California coastal areas. A study of the interactions of the three organisms in the Adelaide area would permit meaningful comparisons with our studies in California. The two natural enemies of *Icerya* have managed to live together in California for 80 years; in Australia this time may be stretched to the thousands of years. A summary of these observations has been written by Quezada (1972).

The simultaneous importation of both vedalia and *Cryptochaetum* into California was a fortunate accident. If only vedalia had been imported at that time, its relative inefficiency in the coastal areas might have been so serious that the subsequent importation of *Cryptochaetum* would have been necessary. This has happened in Bermuda (Bennett and Hughes, 1959) and in some small Caribbean islands (Bennett, 1968). Therefore, we strongly support the policy of importing multiple natural enemies, as exemplified by the case of *Cryptochaetum* and vedalia as control agents for cottony-cushion scale.

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