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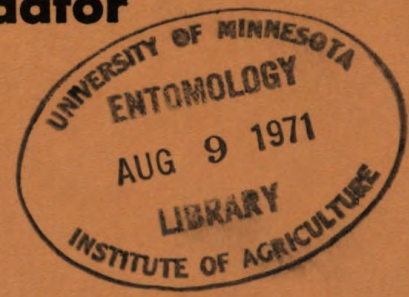
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② TECHNICAL BULLETIN No. 64 DECEMBER 1966

**Predator-Prey Investigations
on the Taro Leafhopper
and Its Egg Predator**



**BARTON M. MATSUMOTO
and
TOSHIYUKI NISHIDA**

① HAWAII AGRICULTURAL EXPERIMENT STATION, UNIVERSITY OF HAWAII

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HONOLULU, HAWAII

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Predator-Prey Investigations on the Taro Leafhopper and Its Egg Predator¹

BARTON M. MATSUMOTO and TOSHIYUKI NISHIDA

INTRODUCTION

Taro, *Colocasia esculenta* (L.), a staple food of the early Hawaiians, was grown in Hawaii for many years without being attacked by insect pests. However, in December, 1930, an outbreak of a new immigrant leafhopper, *Tarophagus proserpina* (Kirkaldy), was discovered at Waianae, Oahu (Fullaway, 1931). Following its initial appearance on Oahu, this leafhopper has spread to all other islands where taro is grown (Fullaway, 1948; Bess, 1953; and Mitchell, 1963).

In 1938, a mirid egg predator, *Cyrtorhinus fulvus* Knight, was imported from the Philippines by D. T. Fullaway and released in taro patches near Kaneohe, Oahu (Fullaway, 1940). This predaceous bug quickly increased in abundance and became widely distributed in its new environment. The scarcity of *T. proserpina* following the introduction of this mirid bug has been attributed to the predatory activity of this insect (Fullaway, 1940).

The prey and predator appear to be native to the Pacific and Indo-Malayan regions. The prey, *T. proserpina*, has been reported to occur in New Caledonia, Guam, Java, Malay Archipelago, the Philippine Islands, Amboina, Australia, New Hebrides, Fiji, Tonga, Niue, the Society Islands, Samoa, the Mariana Islands, Micronesia, and elsewhere in the Pacific (Fullaway, 1931; Swezey, 1936; Williams, 1944; Zimmerman, 1948*b*; and Pemberton, 1954). Recently, it was observed in Amami Oshima Islands, Ryukyu Islands, and Taiwan (Nishida, 1964). Pemberton (1954) believes that the taro leafhopper is probably native to the Malay Archipelago. There appears to be little information on the distribution of *C. fulvus*. This egg predator has been recorded from the Philippine Islands, Java, Fiji, and Samoa (Usinger, 1939; Zimmerman, 1948*a*). In 1947, this predator was purposely introduced to Guam where it has effectively controlled the taro leafhopper there (Pemberton, 1954).

¹ This technical bulletin is part of a thesis submitted by the senior author to the Graduate School of the University of Hawaii in partial fulfillment of the requirements for the Master of Science degree.

Predators are important and interesting biological control agents. Some of the most interesting predators are egg predators in the genus *Cyrtorhinus*, which feed on the eggs of homopterous insects. The present study is concerned with the predator-prey relationships between a species of *Cyrtorhinus* and the taro leafhopper. It is hoped that the results of this study will contribute additional knowledge to the subject of egg predation, a subject which is of considerable interest to those interested in the utilization of egg predators in the biological control of homopterous pests.

GENERAL PROCEDURE

The studies were conducted in the laboratory and in the field. Studies on the biology of the taro leafhopper and the mirid egg predator were conducted in a laboratory where the temperature and humidity conditions were not controlled. Hydrothermograph records indicated that in the laboratory the temperature ranged from 72° to 90°F. and the relative humidity, from 46 to 95 percent.

The taro used in these studies was of the Chinese variety called "bunglong" (Neal, 1948). This variety, called the lu'au taro in Hawaii, is grown for the leaves rather than for the corms. Although both the poi variety and lu'au variety are grown, only the latter variety was used in this study since field observations indicated a higher leafhopper and mirid egg predator population on it than on the poi taro. Furthermore, lu'au taro is not uprooted at each harvest. Only the leaf lamina and a small portion of the petiole still intact are harvested periodically. Therefore, these plants remain in the field for several years, while the poi taro is harvested every 12 to 14 months. For studies of this kind, it is important that the plants remain undisturbed for long periods.

The study area for the field experiments was located in Kahaluu Valley, Oahu, which is situated on the windward side of the island. This area is in the C-1 zone (Ripperton and Hosaka, 1942), in which are found some of the most important areas for crop production. It is located at the mouth of the valley, less than half a mile inland from the ocean. About 30 acres of taro is under cultivation with the majority of the acreage being devoted to the lu'au taro. Since there is a continuous demand for either the corms or the lu'au leaves, the grower harvests and plants frequently. Thus, taro in various stages of development can be found throughout the year.

As lu'au taro is a wetland taro, it must be grown in muddy, specially prepared taro patches which are continuously flooded; and, as in other varieties, it is propagated vegetatively. The suckers are removed from the mother plant at harvest. The corms are cut off, leaving approximately a fourth of an inch of them still intact, and the petioles are cut to about 6 inches in length. The suckers are then planted in the mud about 10 inches apart and in rows about 2 feet apart (figure 1). From this single plant, several lateral suckers develop as the plant matures.

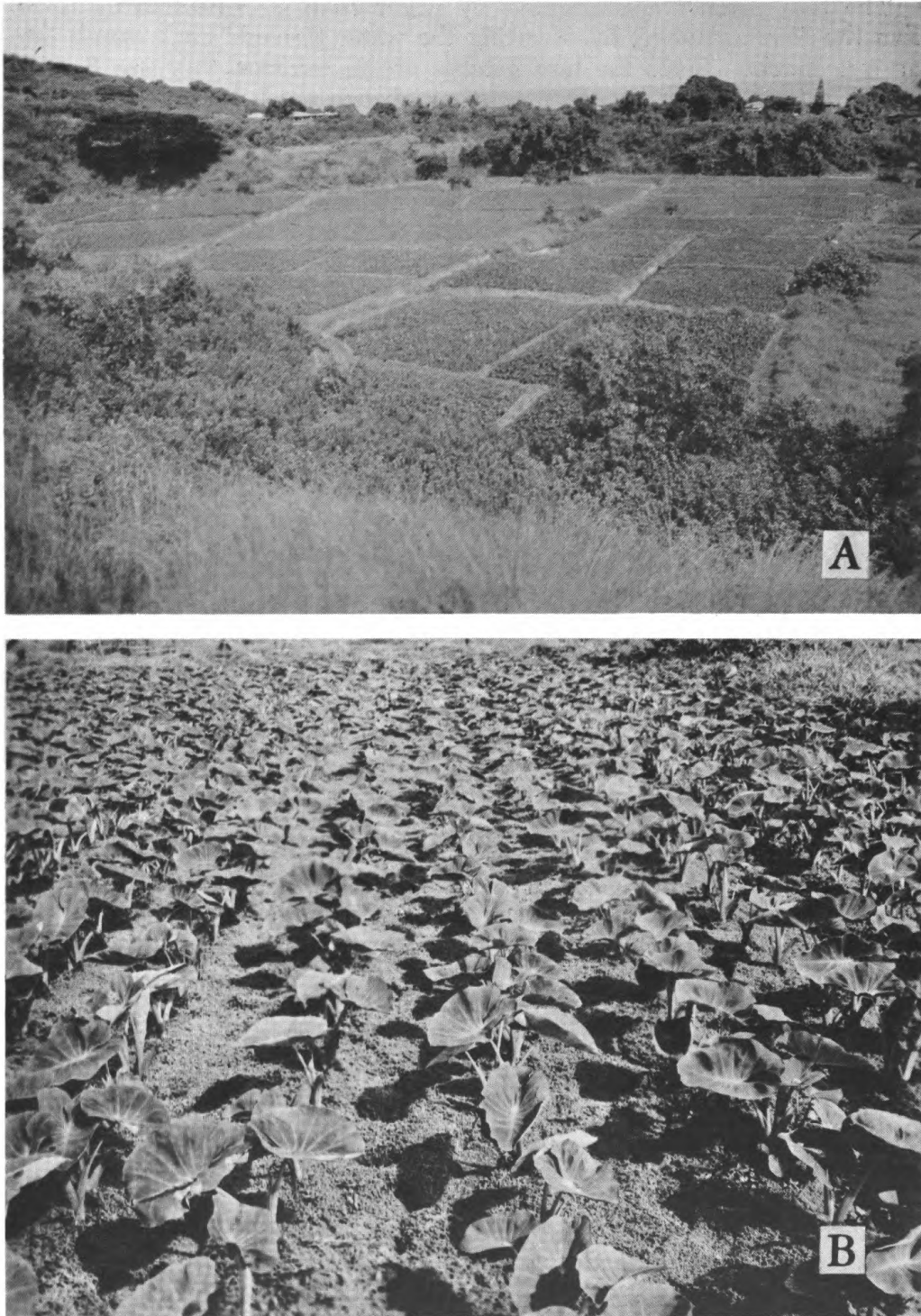


FIGURE 1. The cultivation of lu'au taro in Kahaluu Valley, Oahu. A. General view of the study area showing the taro patches. B. Close-up of a recently planted taro patch.

The taro patches are irrigated by water from streams flowing down from the Koolau Range, by diverting the water through small canals into the taro patches. Since the taro patches are in terraces, they are flooded in such a way that the water flows through one patch into others located at lower levels. In flooding, the water level in the patches is regulated so that the water does not cover the entire taro plant. Usually the water level is regulated so that the water in the patches is maintained at a depth of approximately 4 inches.

The general climatic conditions of the study area are presented in figure 2. The temperature and rainfall data (U. S. Weather Bureau, Climatological Data, Annual Summary, 1957-61) are 5-year means for the years of 1957 to 1961. From the climatological data it is evident that the temperature is relatively uniform throughout the year. The lowest temperature of 70.3° F. occurred during February, and the highest temperature of 76.9° F. during July. Thus the annual difference is only 6.6° F. The annual rainfall patterns are not as uniform as those of the temperature. The highest rainfall was recorded in March with 7.8 inches and the lowest in June with 2.5 inches. The summer months were generally lower in rainfall than the winter and spring months. The rainfall is not as high in this area as in some of the other taro-growing areas; however, water is plentiful because of the heavy rainfall in the Koolau Mountains from whence the streams originate.

In order to obtain a general picture of the micro-environmental conditions in the taro patch, a limited number of measurements were taken by means of a thermocouple (Leeds and Northrup Company) and a Bendix psychrometer. These records, presented in table 1, indicate that the temperatures within the plant tissue, between the leaf grooves, and the air temperatures were similar. The water temperature was slightly lower probably because the water flowed from the cool, high elevations of the Koolau Mountains. The relative humidity under the taro canopy ranged from 77.5 to 79.0 percent, which was lower than anticipated. This low value of the relative humidity may be due to the trade winds blowing in from the ocean and preventing the build-up of atmospheric moisture in the air under the canopy.

GENERAL BIOLOGY OF PREY AND PREDATOR

Prey

The female leafhopper oviposits in the petiole of the taro plant. The mean incubation period of the eggs in the laboratory was found to be 14.5 ± 1.0 days. There are five nymphal instars. The mean duration of the first to the fifth instars was 3.6 ± 0.6 , 3.0 ± 0.3 , 3.1 ± 0.4 , 3.6 ± 0.6 , and 5.1 ± 0.5 days, respectively. Because the relative ages of the nymphal stages of field-collected samples were based on size, it was necessary to take measurements on individuals of known ages in the laboratory. The mean head width and mean body length of the five instars were: first, 0.12

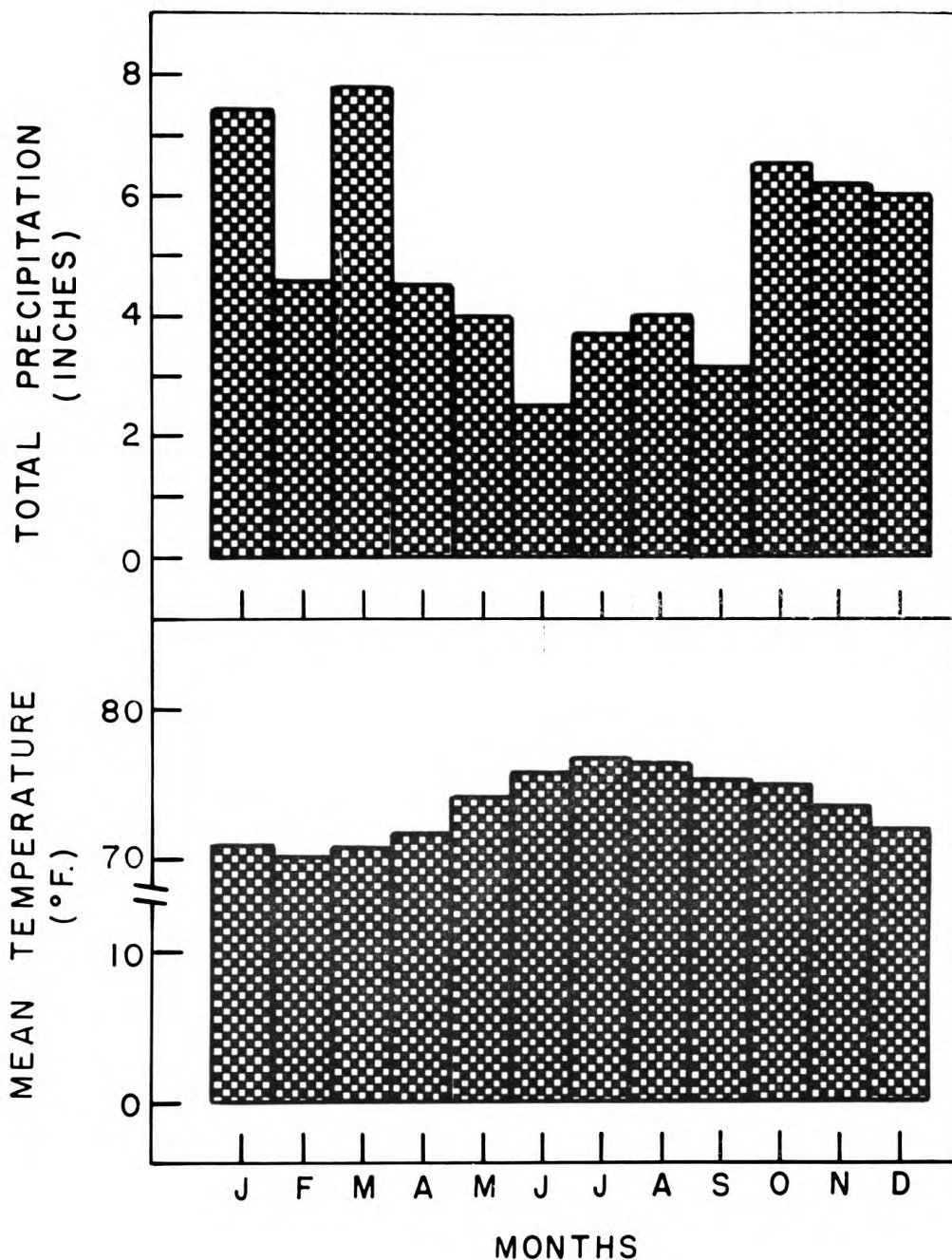


FIGURE 2. A summary of the mean monthly temperature and total precipitation of the Kaneohe Area (U. S. Weather Bureau, Climatological Data, Annual Summary, 1957-61).

TABLE 1. Micro-environmental data of a taro patch (measurements taken on October 17, 1963, from 9:30 to 10:30 A.M.)

LOCATION	POINTS WHERE TEMPERATURE (°F.) READINGS WERE TAKEN				PERCENT OF RELATIVE HUMIDITY	
	In petiole tissue	Between leaf groove	Water	Air temperature (1 inch above water)		Air temperature (1 foot above taro)
1	81.5	83.1	77.0	77.9	81.5	79.0
2	83.3	84.2	78.8	84.2	84.2	77.5
3	82.4	82.4	80.6	80.6	81.0	78.0
Mean	82.4	83.2	78.8	80.9	82.2	78.2

± 0.01 mm \times 1.02 ± 0.07 mm; second, 0.16 ± 0.01 mm \times 1.35 ± 0.15 mm; third, 0.18 ± 0.01 mm \times 1.71 ± 0.07 mm; fourth, 0.27 ± 0.01 mm \times 2.17 ± 0.06 mm; and the fifth, 0.34 ± 0.02 mm \times 2.86 ± 0.17 mm.

The taro leafhopper appears to be host-specific to taro (Fullaway, 1940). During the course of these studies it was not observed on any other plant besides the taro. Observations made in Manoa Valley and Kahaluu Valley showed that the taro leafhopper is abundant on taro grown in the water, but very scarce on dryland taro. Whether the cause of this scarcity was due to natural enemies or to other factors is not known.

The majority of the leafhoppers in the field are usually found in the sheltered, covered axils of the leaves. Nymphs and adults were also observed in the folds of young leaves. The adults and nymphs appear to form aggregations; however, when disturbed they disperse in all directions. Although both brachypterous and macropterous leafhoppers have been reported (Fullaway, 1937), the latter were rarely seen during this study.

An interesting observation made in the field was that the leafhopper was able to hop on the surface of the water. When disturbed, some of the nymphs and adults dropped onto the water, but they hopped off the water very quickly. This ability to "walk" on the water enables the insect to survive in an aquatic environment. It also enables the insect to move from plant to plant.

The female appears to prefer to oviposit in certain parts of the petiole. Examination of taro plants showed that the leafhopper eggs were oviposited all along the leaf petiole, but a larger proportion of the eggs was found in the areas halfway between the bottom of the plant and the lamina.

Taro petioles in which the leafhopper had inserted the ovipositor are easily recognized. After the puncture is made, the plant sap oozes out. Upon drying, there is a dark residue at the puncture. It was noted that the dark spots do not always mean that an egg is present, for the female often inserts her ovipositor into the plant without laying eggs. However, all eggs in the plant tissue were found under the dark spots (figure 3).

The adult female oviposits in a very characteristic manner. Prior to egg deposition, the female extends her ovipositor and shakes her abdomen violently while keeping the rest of her body stationary with the legs grasping the taro petiole. After this preliminary act, the leafhopper inserts the ovipositor into the taro petiole. She often withdraws the ovipositor and then inserts it again. The significance of this act is not known. As stated above, insertion of the ovipositor into the taro tissue does not always result in the deposition of eggs, for an examination of the taro petioles into which the females had inserted the ovipositor showed that eggs were present in some punctures but not in others.

The abdominal vibration such as the one observed in this study was also noted by McMillian (1963) in his work with the leafhopper, *Sogata orizicola*. However, he found that this vibration was related to the mating

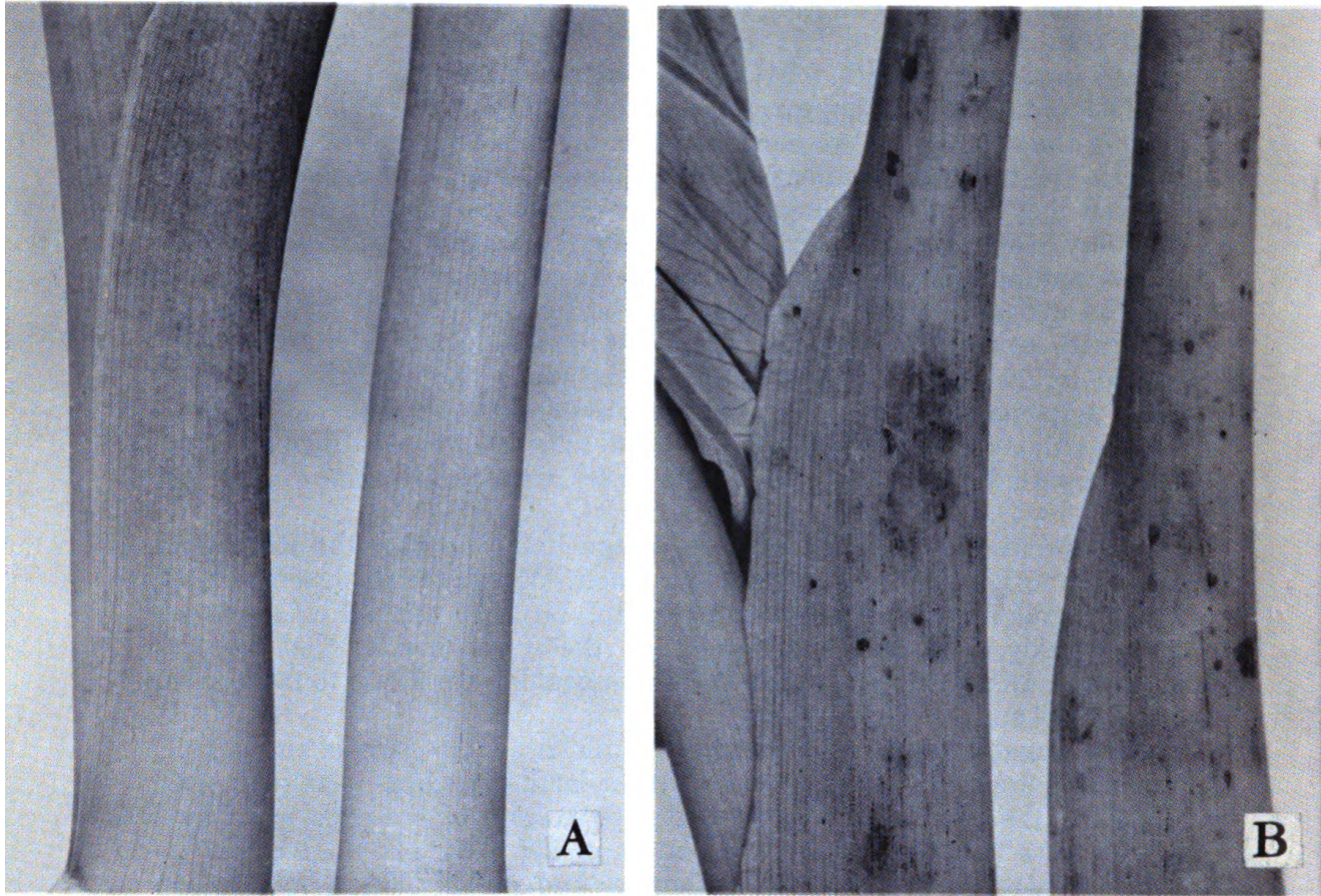


FIGURE 3. Differences in appearance of taro petioles resulting from leafhopper oviposition. A. Clean, unspotted petiole. B. Spots resulting from ovipositional punctures.

behavior rather than to the ovipositional behavior, and that both sexes exhibited this behavior. In this present study, no males were observed exhibiting this behavior.

Predator

Like the taro leafhopper, *C. fulvus* lays its eggs in the tissue of the taro petioles. The mean duration of the egg stage was 13.0 ± 1.0 days. The number of instars appears to vary. Some of the nymphs reached the adult stage in four molts while others completed development after three molts. Of the 63 laboratory-reared individuals, 63.5 percent molted four times and 36.5 percent molted three times. The cause of this variation in the number of molts was not determined. The mean duration of the first to the fifth instars was 3.3 ± 1.1 , 2.9 ± 1.0 , 2.3 ± 0.7 , 2.8 ± 1.1 , and 3.9 ± 0.8 days, respectively. Because the relative ages of the nymphal stages

of field-collected samples were based on size, measurements were taken on individuals of known ages in the laboratory. The mean head width and mean body length of the five instars were: first, 0.17 ± 0.00 mm \times 1.01 ± 0.07 mm; second, 0.25 ± 0.00 mm \times 1.34 ± 0.10 mm; third, 0.32 ± 0.01 mm \times 1.89 ± 0.16 mm; fourth, 0.33 ± 0.00 mm \times 2.22 ± 0.16 mm; and fifth, 0.33 ± 0.00 mm \times 2.51 ± 0.18 mm.

This egg predator appears to be closely associated with the host plant of its prey. Observations made during this study confirm reports made in the literature that it is not associated with plants other than taro. Observations in Manoa Valley showed that it was not present on dryland taro. Whether this absence of the predator was due to the scarcity of its prey is not known.

The predator adults are stronger fliers than the leafhopper adults. When disturbed they can hop and fly away with great rapidity. However, they cannot "walk" on the water like the taro leafhoppers. Without doubt, this ability to hop and fly is a valuable attribute which makes it possible for this predator to disperse rapidly over large areas by moving from plant to plant.

Unlike the taro leafhoppers, the adult and nymphal stages of *C. fulvus* are not gregarious. Although present on plants infested with the taro leafhopper, they were generally found all over the plant. They were also found together with leafhopper nymphs in the folds of the young leaves where no leafhopper eggs were present.

The egg-laying habit of *C. fulvus* is different from that of the taro leafhopper. Unlike the taro leafhopper, the predator does not insert its eggs deeply into the plant tissue. The eggs are partially exposed and the operculum can be readily seen without dissecting the surrounding plant tissue. Evidently the presence of leafhopper eggs affects oviposition, for under laboratory conditions, it was found that oviposition was greater on plants that had the eggs of the prey than on those that did not have any.

Oviposition by the predator is not as obvious as that of the taro leafhopper. Prior to oviposition the insect probes the surface of the taro petiole with its beak. This behavior might be associated with some kind of a "searching behavior" in response to a stimulus or stimuli from the leafhopper eggs in the plant tissue. After this initial behavior the female inserts the ovipositor into the plant tissue. As the ovipositor is inserted, the female drops her abdomen slightly downward so that the sternite of the abdomen appears to touch the surface of the petiole. However, unless one looks closely at the insect, this ovipositional behavior may go unnoticed.

This egg predator feeds on the leafhopper eggs imbedded in the plant tissue by inserting its beak into the egg and sucking out the content. A close examination of the leafhopper eggs dissected from taro petioles showed that it is possible to recognize eggs that had been preyed upon by the predator. The normal, newly laid, unhatched eggs were very turgid, white, and glistening, while those in the later stages of development were

also turgid but were pale white with two reddish spots, which are the ocelli of the developing embryo. On the other hand, eggs that had been preyed upon by the predator were, in general, flaccid. However, the predator does not always suck out the egg content completely. Therefore, the degree of flaccidity varied, depending upon the amount of egg content removed. It was also possible to distinguish eggs that had been preyed upon from those that had hatched. The eggs from which the nymphs had hatched had a longitudinal slit on the anterior end, which was absent in the eggs upon which the predator had preyed.

The feeding habit of *C. mundulus*, the egg predator of the sugar cane leafhopper, *Perkinsiella saccharida*, was studied by Williams in 1932. He also noted that *C. mundulus* punctured many eggs but only few were emptied completely. According to Williams, an undetermined fungus spore enters the egg while it is still in the ovary of the sugar cane leafhopper. This fungus is not harmful to either the egg, nymph, or adult but is harmful to the egg whenever the egg chorion is punctured. As *C. mundulus* does not necessarily suck the leafhopper eggs dry, Williams stated that the fungus infection resulting from the feeding punctures completes the destruction of the eggs not destroyed by the egg wounds made by *C. mundulus*. Whether such microbial agents are involved in the taro leafhopper eggs fed upon by *C. fulvus* is not known.

ASPECTS OF PREDATOR-PREY RELATIONSHIPS

Seasonal Variation in Abundance

An investigation of the seasonal abundance of the taro leafhopper and the mirid predator was conducted by taking monthly samples of these insects for a period of 12 months. Each sample consisted of all the leafhoppers and predators aspirated from a taro stool which included a mother plant and 3 to 6 lateral suckers. Five taro patches, planted linearly adjacent to each other, were used (figure 4). Each sampling plot was located approximately midway on each side of the rectangular-shaped taro patch.

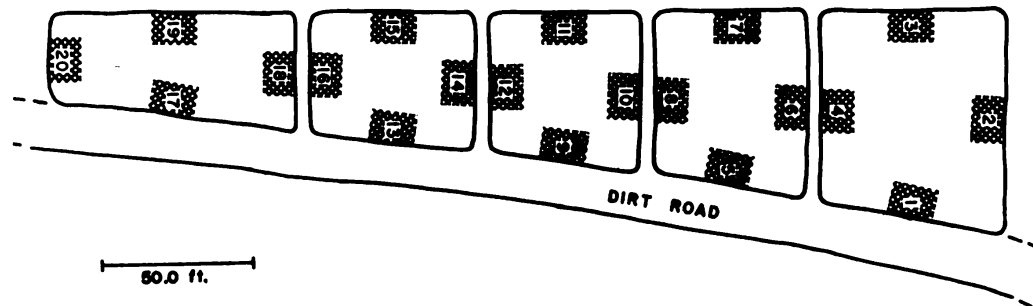


FIGURE 4. Diagrammatic sketch of the experimental taro patches showing the location of the 20 sampling plots.

The stool sampled was located on the third row inward from the edge of the levee or approximately 5 feet from the levee. Sample number 1 was taken from the roadside of the taro patch and succeeding samples were taken in a counterclockwise direction. This was systematically followed in the adjoining four taro patches. The initial sampling was started in August, 1962, and was continued at monthly intervals through the following 12-month period. Although attempts were made to take a prescribed number of samples each month, this procedure was not possible due to unforeseen circumstances. From August, 1962, to April, 1963, a total of 20 monthly samples were taken; however, on April 15, 1963, Kahaluu Valley was inundated as a result of heavy rains which destroyed some of the plots. Thus, from May to July, 1963, the sampling was reduced to 8 samples per month. Upon the termination of the 12-month period a total of 204 samples had been taken. At each monthly collection the samples were brought into the laboratory where the total number of individuals of both species was counted. The mean number of each species per month was obtained by dividing their respective totals by the number of samples. Using these mean values as an index of abundance the graph presented in figure 5 was prepared.

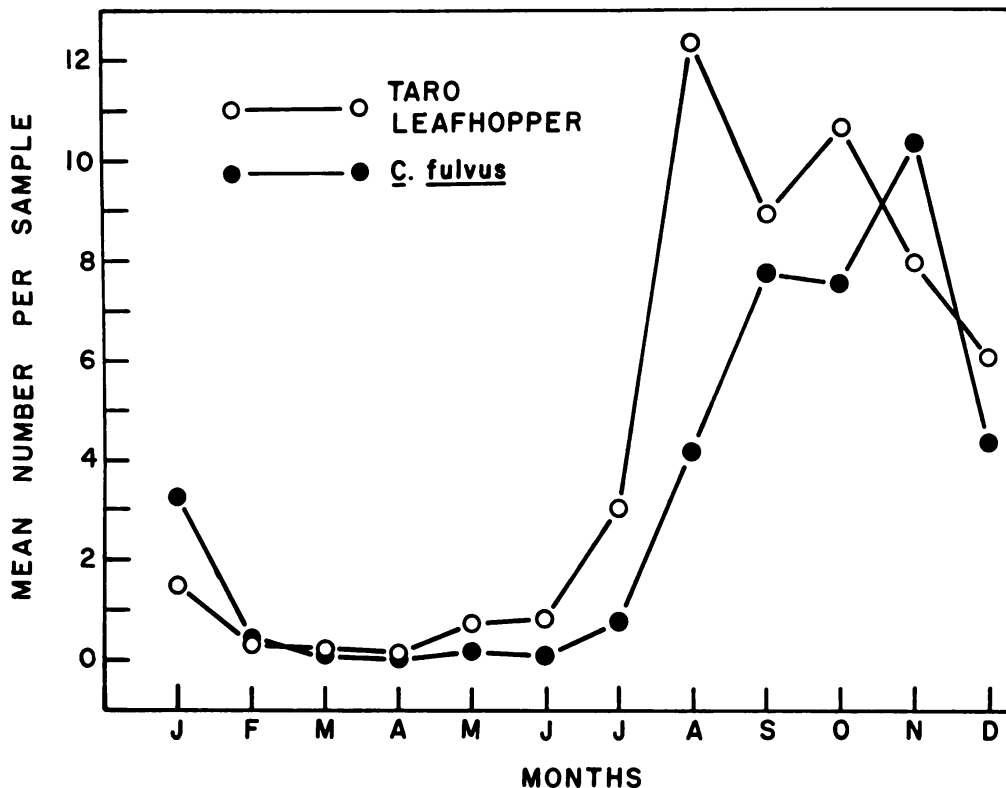


FIGURE 5. Seasonal changes in abundance of the taro leafhopper and *C. fulvus* during 1962-1963 at Kahaluu Valley, Oahu.

From figure 5 it is evident that the population of the taro leafhopper fluctuated considerably throughout the year even though there was only a small annual change in temperature. The population was found to be the lowest during February to June. From then the population increased and reached a peak in October. From then on it declined rapidly until April of the following year.

The population of *C. fulvus* followed a trend similar to that of the taro leafhopper (figure 5). However, with the exception of November and January, the population of the predator remained lower than that of the prey. It is of interest to note that during March and April the populations of both the predator and prey approached zero. However, there was no extinction of either the predator or prey. As the leafhopper started to increase, the population of the predator also increased. The widest gap between the leafhopper and the predator population was observed in August. During this month the leafhopper population increased to a greater level than that of the predator. However, during the succeeding months, the population of the predator increased to such an extent that it approached that of the leafhopper and surpassed it in November. This type

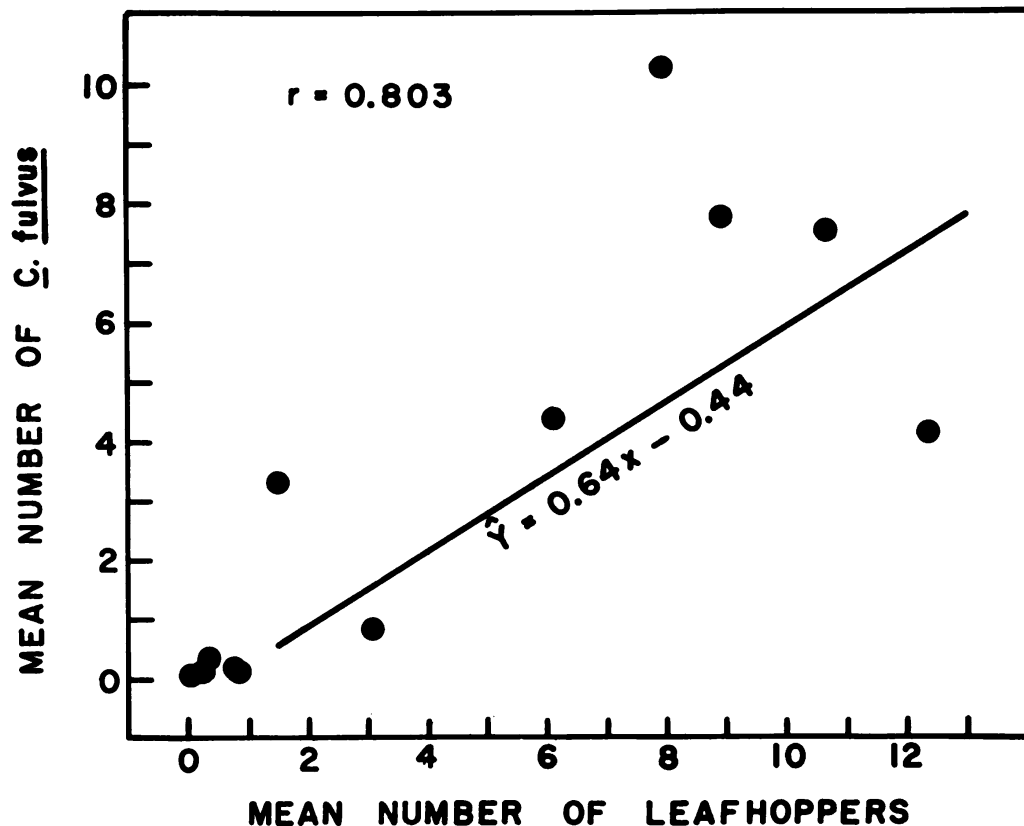


FIGURE 6. Correlation between the population of the taro leafhopper and that of *C. fulvus*.

of predator-prey fluctuation has been observed by other investigators (Huffaker and Kennett, 1956; Huffaker, 1958; MacArthur, 1955; and Utida, 1957).

The effectiveness of a predator in keeping the population of its prey down to a low level depends upon its ability to regulate its numbers in relation to changes in the population of the prey. One may obtain a general idea of the changes of the population of the predator in relation to that of the prey by means of a correlation analysis. Such an analysis was made using the data obtained from all the samples. This analysis gave a correlation coefficient of $+0.803$, significant at the 1 percent level (figure 6).

Seasonal Variation in Sex Ratio

Data on seasonal changes in the sex ratio of the leafhopper and *C. fulvus* were obtained by counting the number of males and females in the samples collected over a period of one year. The data presented in figure 7 are based on the adults for it was not possible to differentiate the sexes in the nymphal stages.

As shown in figure 7, the sex ratio of the leafhoppers fluctuated around the 50:50 percent value during the year. During the months of April, June, and July, the proportion of male and female leafhoppers was equal; however, during March and September, the males appeared to be relatively scarce. The highest percentage of females, 54.5 percent, was found during September. Utilizing the data in figure 7, a chi-square analysis was made on the assumption that the sex ratio in the natural population was 1:1. There was a significant deviation from the assumed sex ratio only during 3 out of the 12 months; viz., January, February, and October. During these months, there was a preponderance of males, 61, 62, and 65 percent, respectively.

The data on the sex ratio of the predator, presented in figure 7, indicate the extent of fluctuation in sex ratio. No data are given for the months of April and June because the overall population of adults during these months was so low that no adults were collected. The data on the 10-month period indicated that the percentage of females was lowest during January, March, July, September, and October. However, the percentage of females was high, above the 50 percent value, during February, May, August, November, and December. There appears to be no consistent trend in the seasonal predominance of either sex, except during May, when the population consisted of only females. As in the case of the leafhopper, a chi-square analysis was carried out.

A comparison of the data on sex ratios of the taro leafhopper and *C. fulvus* indicates considerable differences; however, the causes of these differences are not known. Figure 7 indicates marked changes in the sex ratio of *C. fulvus* but relatively little changes in the case of the taro leafhopper. Furthermore, the population of the predator appears to be pre-

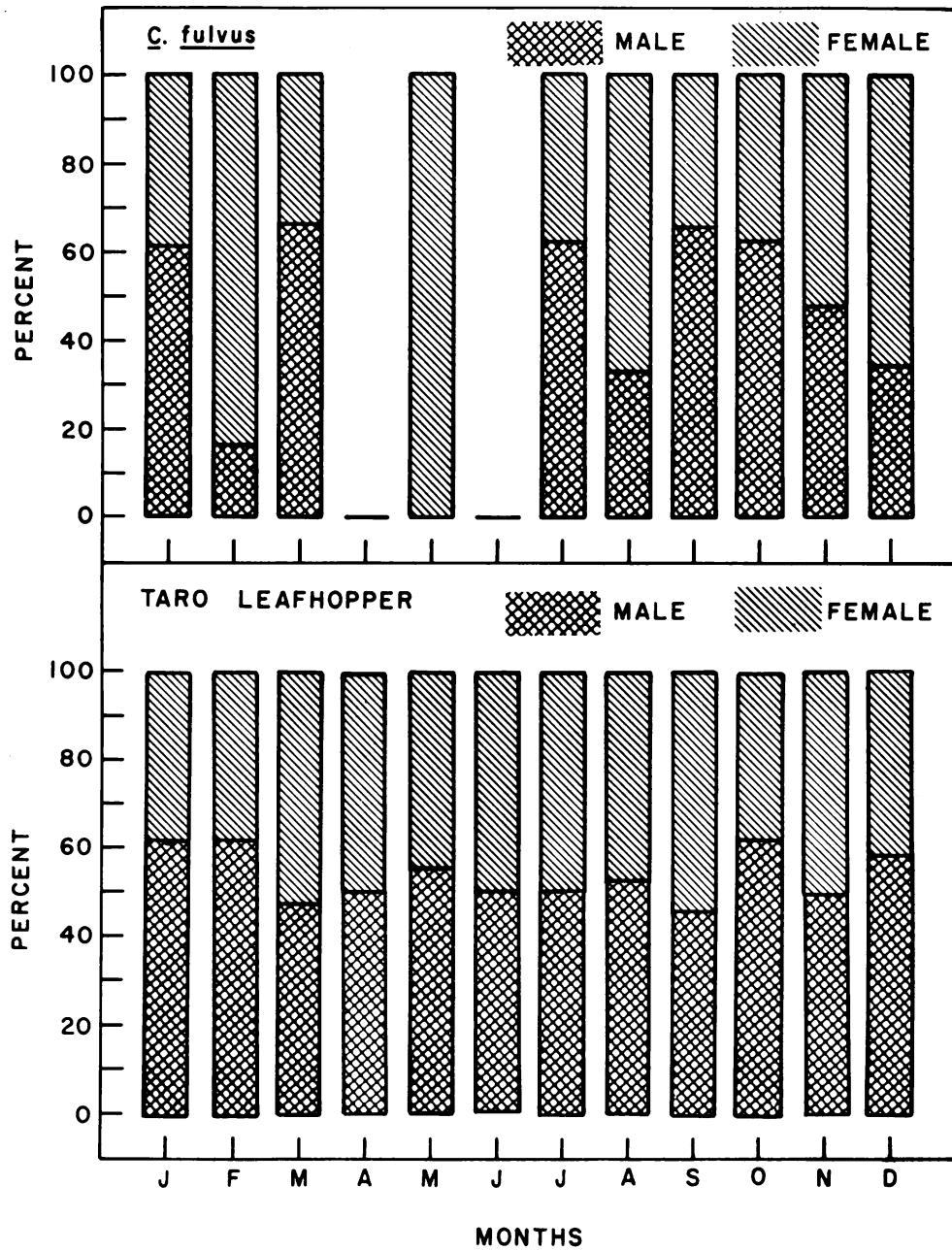


FIGURE 7. Seasonal changes in the proportion of the sexes of the taro leafhopper and *C. fulvus* at Kahaluu Valley, Oahu, during 1962-1963.

dominantly female when the population is low while in the case of the taro leafhopper the sex ratios appear to be independent of population density.

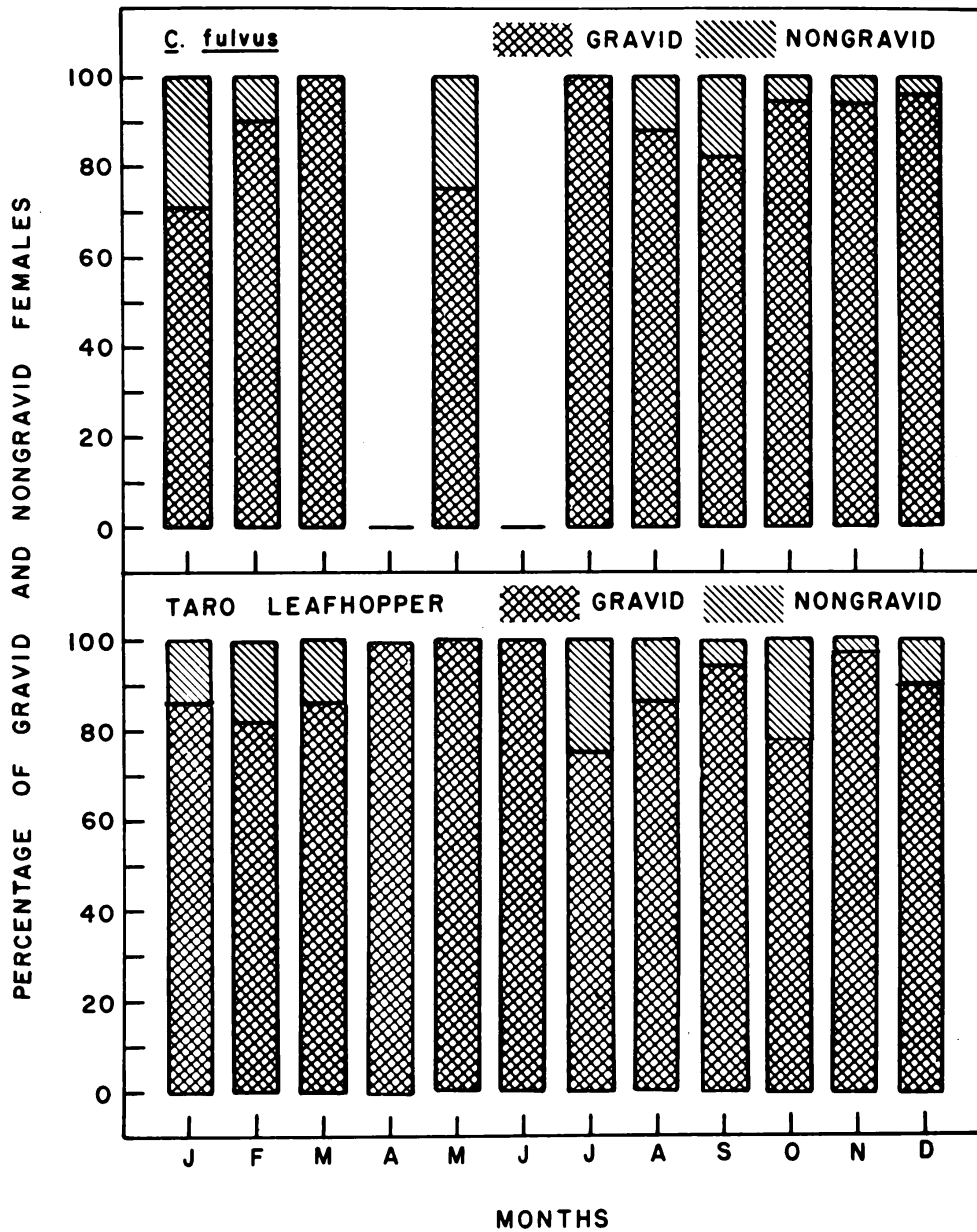


FIGURE 8. Seasonal changes in the gravidity of the taro leafhopper and *C. fulvus* at Kahaluu Valley, Oahu, during 1962-1963.

Seasonal Variation in Gravidity

Seasonal changes in the gravidity of the taro leafhopper and *C. fulvus* were determined by examining the individual specimens collected at each monthly interval throughout the year. The females in the samples

were segregated and dissected under a binocular microscope. The number of gravid and nongravid females were counted and recorded. All individuals containing one or more fully developed eggs were considered gravid, while those having no mature eggs were considered nongravid.

The data obtained indicated that the percentage of gravid leafhoppers fluctuated during the year (figure 8); however, the percentage was consistently higher than for the nongravid individuals throughout the year. The lowest level of gravid leafhoppers was found in July at which time they constituted 75.0 percent of the total female population. In contrast to this, during the previous 3 months of April, May, and June, 100.0 percent of the leafhoppers were gravid while during the other 8 months of the year the percentage fluctuated between 77.1 and 97.2 percent.

The seasonal changes in the gravidity of *C. fulvus* were not similar to those of the leafhopper. During the months of April and June the population of predators was so low that no adults appeared in the samples. This was in sharp contrast to the high percentage of gravid leafhoppers that were present during these same months. During March and July, *C. fulvus* was found to be 100.0 percent gravid, while during these same months the leafhoppers were 85.7 and 75.0 percent gravid, respectively. The percentage of gravid leafhoppers and predators was almost equal during August, but the greatest difference was found during the months of April and June. Although the number of gravid leafhoppers and *C. fulvus* varied from month to month the annual mean percent gravidity was very close. The mean gravidity of the leafhopper was 89.2 percent while that of the predator was 89.0 percent.

Age Structure

It has been shown that the population of the taro leafhopper and *C. fulvus* fluctuated to a considerable extent throughout the year. Since these fluctuations are related to birth and death rates it appeared desirable to obtain information on the population age structure. An attempt was therefore made to obtain data on the age structure of the predator and prey by examining the samples collected throughout the year.

All the leafhoppers and predators sampled during 1962–63 were examined and placed into six age categories based on developmental stages: 1st instar, 2nd instar, 3rd instar, 4th instar, 5th instar, and adult. Although the exact ages were unknown, it was felt that, in the absence of other means of determining age, these categories would serve a useful purpose for they do represent relative ages of the individual. The information obtained from laboratory studies on the biology of the respective insects was found useful in placing the field-collected material into the various age categories. The results of these studies are presented graphically in figure 9.

An examination of the data on the age distribution of the taro leafhopper shows several points of interest. It may be noted that in general

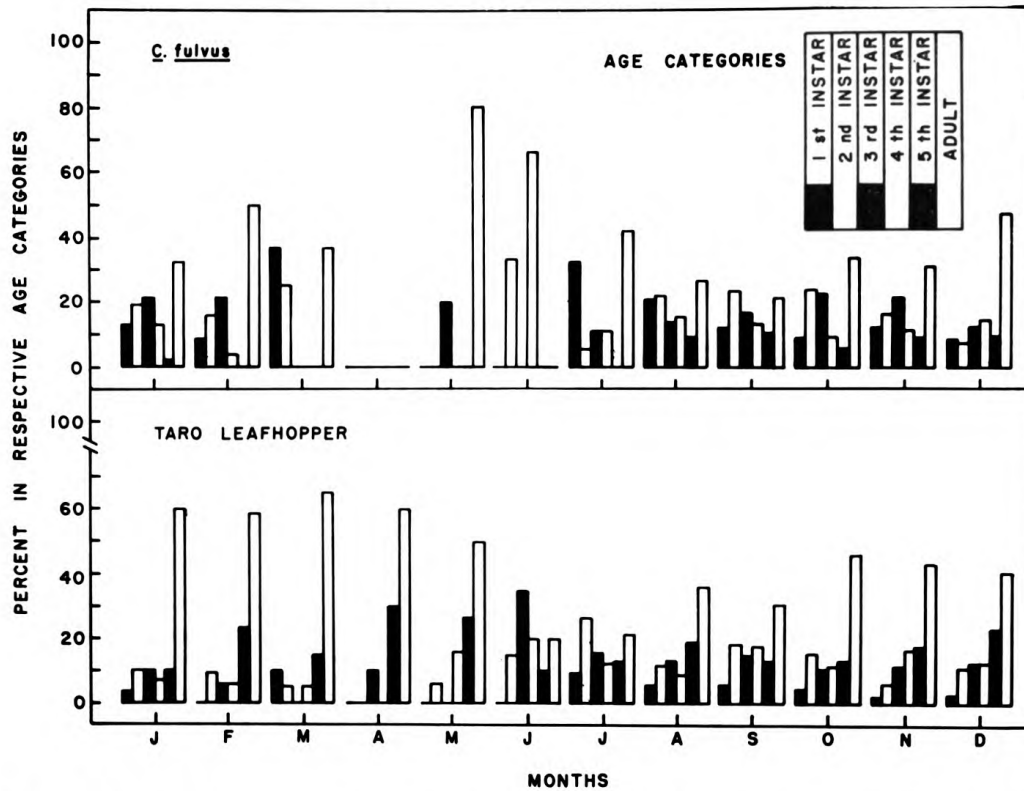


FIGURE 9. Age distribution of the taro leafhopper and *C. fulvus* population at Kahaluu Valley, Oahu. Samples collected during 1962–1963.

there was a high proportion of adults throughout the year; however, the proportion of adults appeared to be highest during January to April. Nymphs of various instars were also present throughout the year. They constituted the highest proportion of the population during June to December. From the data presented it is also evident that the proportion of the first instar nymphs was consistently low throughout the year. First instar nymphs were not present during April to June.

The data on the age structure of *C. fulvus*, presented in figure 9, show considerable changes during the year. The adults were present throughout every month of the year with the exception of April and June. The proportion of adults was highest during May. Nymphs of various instars were generally present throughout the year except during April. First instar nymphs were not present during April, May, and July.

A comparison of the age structure of the taro leafhopper and that of *C. fulvus* shows that the absence of the first instar nymphs of the predator was correlated with the absence of the first instar nymphs of the prey. For example, from April to June there were no first instar nymphs of the taro leafhopper. During the same period the first instar nymphs of the

predator also were not present. The absence of first instar nymphs of the leafhopper indicates that the eggs were not hatching, possibly because of the predatory activity of *C. fulvus*. The absence of the first instar nymphs of *C. fulvus* also shows that this predator was not laying eggs, possibly because of the scarcity of food. Laboratory observations showed that *C. fulvus* lays more eggs in petioles which contained leafhopper eggs than in those without leafhopper eggs.

Spatial Distribution

Field studies made during this study showed that the taro leafhopper and *C. fulvus* were widely distributed wherever taro is grown. However, although all taro patches look superficially alike, there were considerable variations in the abundance of these insects. In Kahaluu Valley, for example, these insects were numerous in some sections of the taro patches but were so scarce in others that it was difficult to collect them.

A study of the spatial distribution was made to determine how the taro leafhopper and *C. fulvus* were distributed within individual taro patches. Data on the spatial distribution of the taro leafhopper and the predator were obtained from three taro patches; two were rectangular in shape and measuring approximately 117.5 ft \times 127.5 ft and 115 ft \times 140 ft, respectively. The third patch was trapezoidal and its dimensions were 130.5 ft \times 65 ft \times 87.5 ft \times 67 ft. To obtain data on spatial distribution, samples of the leafhopper and the predator were taken from taro stools

TABLE 2. The relative abundance of the taro leafhopper and *C. fulvus* along the peripheral and interior areas of taro patches

PATCH NO.	INSECT	MEAN NUMBER PER STOOL		"t TEST" t VALUES
		Periphery	Interior	
1	Taro leafhopper	10.4	7.4	0.845
	<i>C. fulvus</i>	8.2	1.5	3.045*
2	Taro leafhopper	32.4	4.7	3.506**
	<i>C. fulvus</i>	5.4	1.4	2.353*
3	Taro leafhopper	9.4	8.1	0.241
	<i>C. fulvus</i>	2.5	0.4	1.400

* Significant at the 5 percent level.

** Significant at the 1 percent level.

at various localities within the taro patches. One series of samples was taken around the peripheral margins and the other from stools located in the central areas of the taro patches. From each taro patch a total of 16 samples was taken, 8 from the periphery and 8 from the central areas.

The data obtained, presented in table 2, indicate that there was considerable variation in abundance of the taro leafhopper and *C. fulvus* within the same taro patches. In taro patch no. 1, there was no significant difference in the leafhopper abundance between the peripheral and central areas, but the difference was significant in the case of the predator. In taro patch no. 2, the population of both the taro leafhopper and the predator was higher in the peripheral than in the interior areas; differences in the leafhopper population being significant at the 1 percent level and that of the predator at the 5 percent level. In taro patch no. 3, there were no significant differences in both the leafhopper and predator abundance between the interior and peripheral areas. Although these differences were not consistently significant, in general it may be noted that the populations of the leafhopper and predator were more numerous along the peripheral than in the interior areas. A typical distributional pattern of leafhopper and predator population is shown diagrammatically in figure 10.

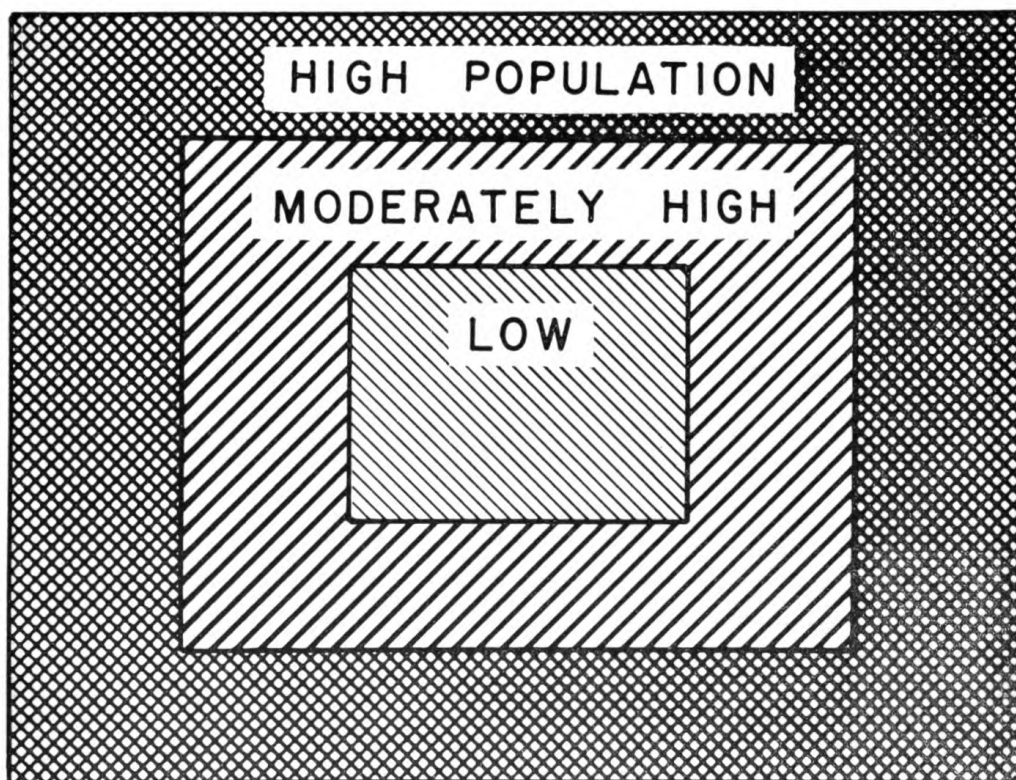


FIGURE 10. Diagram showing the relative density of the taro leafhopper and *C. fulvus* in a taro patch.

In order to obtain a clearer picture on the distributional relationship between the taro leafhopper and *C. fulvus*, the field data were subjected to a correlation analysis by pooling all the data obtained from the three taro patches. This analysis gave a correlation coefficient of $+0.448$ (23 d.f., significant at 5 percent) which shows a significant relationship between the spatial distribution of the leafhopper and its predator. These data indicate that the dispersal patterns of the prey and predator are closely related.

Egg Predation and Prey Population

In this study, an attempt was made to obtain information on the extent to which *C. fulvus* can suppress the population of the taro leafhopper. The method used was the "removal technique" in which the predators were removed from some plots by use of an aspirator while in others they were left alone. This procedure has been used by other investigators (Fleschner, 1952, and Huffaker and Kennett, 1953) in the evaluation of the effectiveness of natural enemies.

The results of this experiment were obtained from eight plots located in two taro patches. Each taro patch contained four rectangular sampling plots about 8 ft \times 12 ft, one on each side of the rectangular taro patch. Each sampling plot contained about 84 stools of taro plants; however, the actual counts were taken from 20 stools located in the middle of the

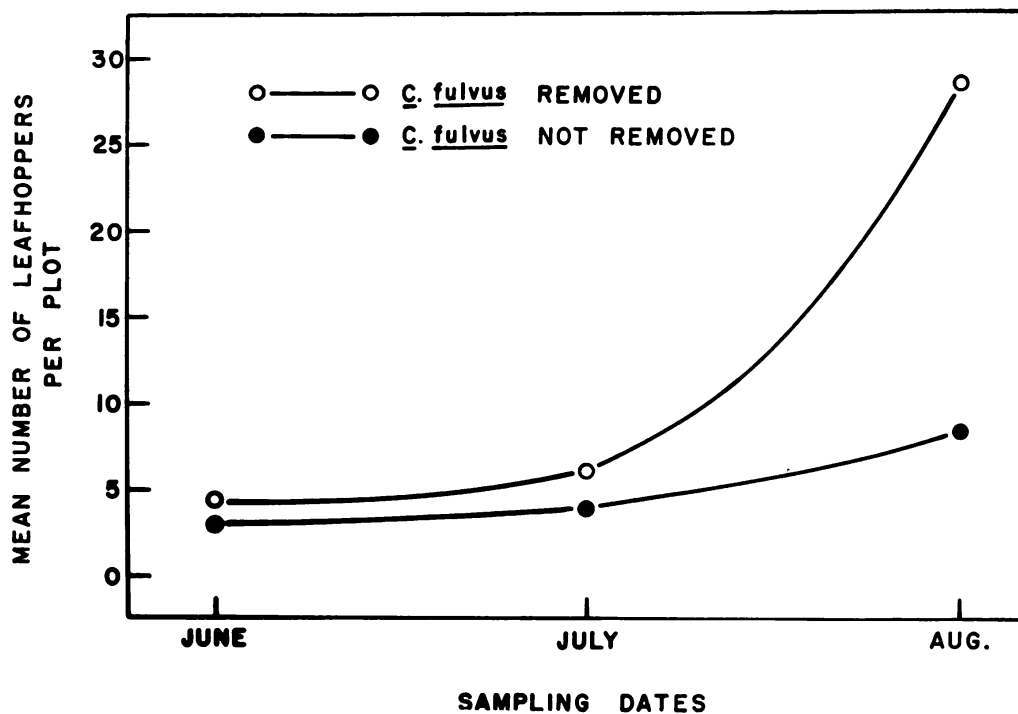


FIGURE 11. The effect of *C. fulvus* on the population of the taro leafhopper.

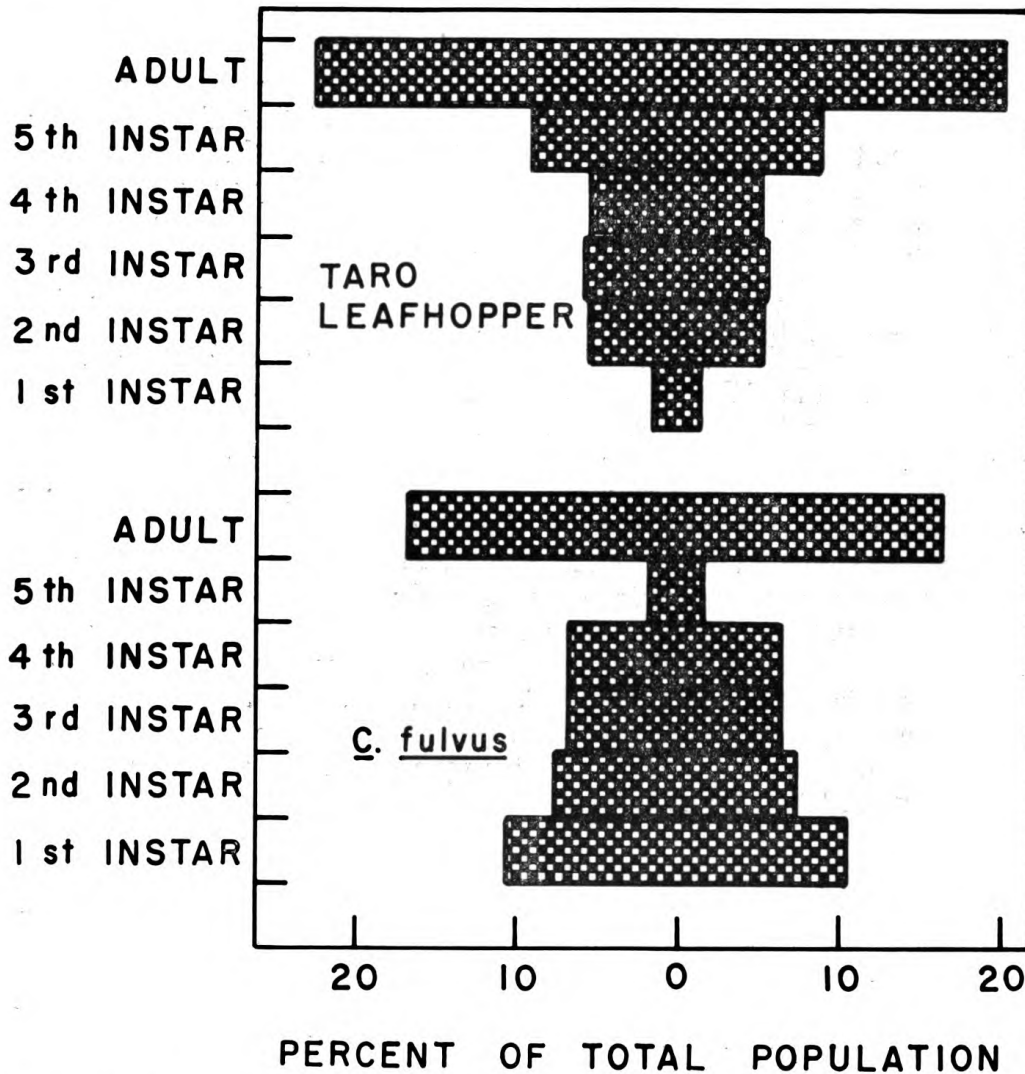


FIGURE 12. Composite age structure of the taro leafhopper and *C. fulvus* based on samples collected during 1962–1963 at Kahaluu Valley, Oahu.

sampling plot. The plants in four plots were examined approximately every other day. At each examination all individuals of the predator, when present, were removed. In the remaining four plots the egg predators were not removed. Data on the population of the taro leafhopper were taken once a month. The experiment was started in June and terminated in August. This procedure obviously did not keep the experimental plots completely free of predators; however, the population of the predator was kept at a lower level than that of the control plots.

Figure 11 presents a graphic picture of the differences in the leafhopper population trends between plots from which the predator was removed and

those from which the predator was not removed. In both plots the population increased only slightly during June and July; however, during August the population in plots from which the predators were removed showed a marked increase. An analysis of variance indicated that the population between the two plots did not differ significantly during the first 2 months. However, during August the population of the leafhoppers in plots from which the predator was removed was significantly higher than that in plots from which the predator was not removed.

The results of this experiment showed increasingly greater differences in leafhopper population with time between plots from which the predator was removed and the control plots. At the termination of the experiment, after 3 months, the difference between the treated and the control plot was significant at the 5 percent level. Judging from the trends of the population curves it appears that if this experiment were continued for a longer period of time and if the removal of the predators had been complete a considerably greater difference might be expected.

Further evidence on the effect of *C. fulvus* on the population of the taro leafhopper can be obtained by an analysis of the age structure of the two insects. The composite age structure, presented in figure 12, shows that the first instar nymphs of the taro leafhopper represented only a small proportion of the total population. However, the first instar nymphs of *C. fulvus* represented a fairly high proportion of the total population. The small proportion of the first instar nymphs of the prey is evidently due to egg predation by *C. fulvus*.

DISCUSSION

Studies on spatial distribution indicated that although the taro leafhoppers were found throughout the taro patch, they were most abundant along the peripheral areas. This type of distribution resulted even though the taro patch with its uniform rows of plants appears to be a very homogeneous environment. Furthermore, one would expect a lower population along the periphery than the interior areas because the usually weedy levees harbored natural enemies usually not present in the interior areas. These enemies include coccinellids and spiders of various species. Ants, which feed on the honeydew of the leafhoppers, have been observed to be more prevalent along the periphery than the interior. However, the relationship between ants and leafhopper abundance is not known. They apparently do not influence the population of *C. fulvus* to any great extent for this predator was also abundant along the periphery of the taro patches. It is possible that this type of distributional pattern is related to the dispersal habits of the leafhopper. Apparently they have an inherent tendency to disperse radially in all directions and, because of the levee, the leafhoppers are stopped from moving farther. This explanation is only tentative. Further studies on dispersal should be made before this type of distribution is clarified.

The problem of evaluating the effectiveness of predators and parasites is one of the difficult problems in a biological control project. The current study on *C. fulvus* was no exception. However, general observations made in the past as well as the information obtained in the present study indicate that *C. fulvus* is effective in keeping the population of the taro leafhopper to subeconomic levels. The observations of Fullaway (1940) showed that prior to the introduction of *C. fulvus* into Hawaii the population of this leafhopper was so high that the taro plants were severely damaged. However, following the introduction of *C. fulvus* the population of the leafhopper was markedly reduced so that injury to the taro plants no longer occurred. In addition to these observations, the following information obtained in this study also supports the viewpoint that *C. fulvus* is an important biological control agent: (1) *C. fulvus* population fluctuations were highly correlated with those of the leafhopper; (2) the spatial distribution of the predator and prey was correlated indicating that the predator was following its prey wherever it went; (3) hand removal of the predator resulted in an increase in the prey; and (4) the age distribution of the taro leafhopper indicated a low proportion of nymphs, especially the younger individuals.

Having presented evidences on the effectiveness of *C. fulvus* in keeping the population of taro leafhopper down to subeconomic levels, it seems desirable to discuss some of the biological attributes which make this predator so effective. The adults possess the ability to disperse rapidly from plant to plant. Because of this power of dispersal they can follow the leafhopper wherever it goes. The almost monophagous feeding habit of nymphs and adults is also an asset. Thus their predatory activity is restricted to the taro plant which in turn is the only known host of the taro leafhopper. This predator is also capable of surviving under conditions of low leafhopper population density when food is scarce. Another important attribute is that *C. fulvus* lays its eggs in the vicinity of the leafhopper eggs and the newly emerged nymphs begin feeding on the leafhopper eggs soon after hatching.

The permanency of predator-prey oscillations has been studied by such workers as Gause (1934), Gause *et al.* (1936), Huffaker and Kennett (1956), and Huffaker (1958). As a result of these studies, the concept of "refuge" and "spatial heterogeneity" as a means of maintaining predator-prey equilibrium has been developed. According to this concept the environment must be heterogeneous so that there are protective sites in which the prey is partially protected against predation. Without such sites the prey will be completely eliminated and the predator itself will ultimately be eliminated through starvation. If, however, there are a certain number of protective sites the predator will not be able to eliminate the prey. In the meantime some of the predators will be eliminated through the lack of food. As the number of predators declines the number of prey

increases again. Through such density-dependent mechanism, the predator-prey equilibrium can be maintained.

The predator-prey relations between *C. fulvus* and the taro leafhopper have not been fully investigated and thus one can only speculate on the mechanisms involved. From biological studies it is known that *C. fulvus* lays eggs in the vicinity of the taro leafhopper. Upon emerging the nymphs feed on the eggs of the taro leafhopper. On individual stools of taro, the leafhopper eggs may be completely devoured because there are no protective sites. However, the nymphs of *C. fulvus* cannot move onto other plants because of the water surrounding the plants. Thus *C. fulvus* may feed on eggs of its own species under conditions of food scarcity while others may die of starvation. The brachypterous leafhoppers have the ability to either "walk" on the water or hop to other stools of taro where they lay eggs. In the meantime the adults of *C. fulvus*, being active fliers, move on to the stools where the leafhopper eggs are present and they in turn oviposit in the same plant. However, in the meantime the leafhopper eggs that have escaped predation hatch and the nymphs from these eggs develop into adults. Through such shifts in the leafhopper and predator population from plant to plant, complete extinction of the prey does not occur. In other words, this shift in population of the predator and prey affords the prey a refuge that appears to be necessary for a predator-prey oscillation system.

In addition to egg predation by *C. fulvus*, there are other mortality factors of minor importance. Coccinellids and spiders feed on the adults and nymphs of the taro leafhopper. However, these predators, not being host-specific, also feed on *C. fulvus* as well as other insects. The parasitization of the eggs of the taro leafhopper by a eulophid, *Ootetrastichus megameli* Fullaway, was reported by Zimmerman (1948*b*). This parasite, however, was not observed during the present study. Floods may at times destroy the taro leafhopper in the low-lying areas where drainage facilities are not adequate. In such situations the extent of mortality caused by flooding depends to a certain extent on the variety of taro. On the short varieties, such as the lu'au taro, the mortality is high because they are completely covered by water. However, on the taller poi variety the plants are usually not completely covered by water. The leafhoppers on such plants crawl up the plant and remain above the water line. This differential drowning effect was observed during the flood of April 15, 1963, in Kahaluu Valley where the short variety was completely covered while the tall variety was only partially covered by water. Observations made a day after the flood indicated that there were no leafhoppers and *C. fulvus* on the short variety, but these insects were present in moderate numbers on the taller poi variety.

SUMMARY

The present study was concerned with the biology of the taro leafhopper, *Tarophagus proserpina*, and its egg-predator, *Cyrtorhinus fulvus*, and certain aspects of the predator-prey relationship between the predator and prey. The biological studies were carried out in the laboratory and the field studies at Kahaluu, Oahu, during 1962-63.

Biological studies showed that the average duration of the various stages of development of the taro leafhopper was as follows: eggs, 14.5 ± 1.0 days; nymphs, first instar, 3.6 ± 0.6 days; second instar, 3.0 ± 0.3 days; third instar, 3.1 ± 0.4 days; fourth instar, 3.6 ± 0.6 days; and fifth instar, 5.1 ± 0.5 days. The mean duration of the various stages of development of the predator, *C. fulvus*, was as follows: eggs, 13.0 ± 1.0 days; nymphs, first instar, 3.3 ± 1.1 days; second instar, 2.9 ± 1.0 days; third instar, 2.3 ± 0.7 days; fourth instar, 2.8 ± 1.1 days; and fifth instar, 3.9 ± 0.8 days.

Field studies on the taro leafhopper and *C. fulvus* showed that the populations of the predator and prey fluctuated throughout the year. In general, the leafhoppers were most abundant during the latter half of the year and relatively scarce during the first half of the year. The population of the predator followed a similar general trend; however, with the exception of November, 1962, and January, 1963, it remained at a lower level of abundance than the leafhopper. A correlation analysis between the abundance of the predator and prey gave a value of $+0.803$ that was significant at the 1 percent level. Such a correlation suggests that the population of the taro leafhopper was being influenced by *C. fulvus*.

Studies on spatial distribution indicated that the taro leafhopper and *C. fulvus* were not spread homogeneously throughout a taro patch. Although the leafhopper was found throughout the taro patch, it was generally more abundant along the peripheral areas than in the central areas. The distribution of the predator followed a similar pattern. A significant correlation coefficient of $+0.448$ was obtained between the abundance of the predator and prey, an indication that the predator was following its prey.

The data obtained on the seasonal changes in the sex ratio indicated considerable differences between the taro leafhopper and the predator. Throughout the year, there were only slight variations in the sex ratio of the taro leafhopper. However, the sex ratio of the predator showed marked changes which appeared to be related to population density. The population of this predator was predominately female when the population was low and male when the population was high.

It was found that the population and the percentage of gravid leafhoppers and *C. fulvus* varied from month to month. In both species the population of the gravid females was consistently higher than that of the nongravid. However, the mean annual percent gravidity of both species

was very close. The mean annual gravity of the leafhopper was 89.2 percent while that of *C. fulvus* was 89.0 percent.

An attempt was made to determine the effect of the predator on the population of the prey utilizing the "removal technique" in which *C. fulvus* was removed from some plots and not in others. The data obtained indicated a rapid increase in leafhopper population in plots from which *C. fulvus* was removed. In the control plots the leafhopper population showed only a slight increase.

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