Spatial Distribution of Mediterranean Fruit Fly (Diptera: Tephritidae) throughout West Oahu: Development of Eradication Strategies

ROGER I. VARGAS¹ and TOSHIYUKI NISHIDA²

ABSTRACT

Distribution of Mediterranean fruit fly, Ceratitis capitata (Wiedemann), throughout west Oahu was determined from trap and fruit infestation data. The range of C. capitata is wider than previously reported and includes four of the five major vegetation zones. No flies were captured in native forests. From November 1985 to October 1986, 96.2% of the traps in xerotropic habitats and 61.5% of the traps in pluviotropic habitats caught flies. During the 12 month study 90.4% of the total flies captured were recovered in 5 traps (total traps = 52) located in or near feral coffee, Coffea arabica L., in Makaha and Waianae Valleys. C. capitata occurred at low densities throughout the year along most of the coastline where residential backyard hosts were infested and sporadically throughout gulches and uplands of the Waianae Mountain Range where common guava, Psidium guajava L., and strawberry guava, Psidium cattleianum Sabine, were infested. The most important hosts were coffee; false kamaui, Terminalia catappa L.; mock orange, Murraya exotica L.; citrus, Citrus spp.; common guava and strawberry guava. Coffee produced as many as 234 flies per kg, while all other host fruits produced low numbers. Findings are discussed with respect to development of eradication strategies for C. capitata in Hawaii.

KEYWORDS: Ceratitis capitata, Tephritidae, fruit fly, population behavior, distribution, eradication.

In the United States, the Mediterranean fruit fly, Ceratitis capitata (Wiedemann), occurs only in Hawaii. Despite strict quarantine procedures designed to exclude this important pest, it has gained entry into the U.S. mainland on a number of occasions and was eradicated, sometimes at great public expense. For example, final cost of the 1980 California program for eradication of C. capitata was over $100 million (Jackson and Lee 1985). Elimination of C. capitata as well as three other economically important fruit fly species from Hawaii would not only benefit mainland agriculture but also encourage commercial expansion of Hawaii's fruit and vegetable industry.

C. capitata is concentrated in small patches throughout the major Hawaiian Islands (Nishida et al. 1985). Because of this limited distribution and abundance, the sterile insect release method (SIRM) appears to be an ideal

¹Tropical Fruit and Vegetable Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, P.O. Box 2280, Honolulu, Hawaii 96804.
²Department of Entomology, University of Hawaii, 3050 Maile Way, Honolulu, Hawaii 96822.
tool for eradication. Furthermore, SIRM is the only currently available eradication technology for *C. capitata* that poses no threat to Hawaii’s environment. Previously we found a distinct spatial distribution pattern for *C. capitata* on the island of Kauai, where populations were concentrated in rain shadow and adjacent upland areas on the east side of the island (Vargas et al. 1983a).

The objective of the present study was to extend investigations of *C. capitata* distribution patterns in order to develop eradication strategies for all of the Hawaiian Islands. West Oahu was chosen for two reasons: first, the area contains the four major vegetation zones in which *C. capitata* has been reported in Hawaii and is representative of other areas, and second, the area would be the next eradication unit south of Kauai, if an eradication program is implemented which begins at the north end of the Hawaiian Island chain.

**MATERIALS AND METHODS**

**Study Area.** Oahu, the third largest island (1574 km²) in Hawaii, consists of the western Waianae Mountains and the eastern Koolau Mountains, connected by a central plateau. These mountain ranges are remnants of the heavily eroded Waianae and Koolau shield volcanoes. This study was conducted in the western Waianae Mountains and the surrounding areas.

West Oahu (Fig. 1) includes the Waianae volcanic region. To the west of the Waianae Mountains are a series of large valleys (Makua, Makaha, Waianae and Nanakuli) and a long coastal band known as the Waianae Coast. To the south is the Ewa Plain, to the east is the Central Plateau, and to the north is the Mokuleia Coast.

On the basis of climate and flora, Ripperton and Hosaka (1942) divided west Oahu into four major vegetation zones: A, B, C, and D with two subzones (D₁ and D₂) in D. With reference to rainfall, xerotropical zones (A and B) occur almost exclusively along the Mokuleia Coast, Waianae Coast and Ewa Plain; whereas pluviotropical zones (C and D) occur primarily as concentric bands about the highest peak on Oahu, Mt. Kaala (1125 m). The C and D zones, characterized by an abundance of common guava, *Psidium guajava* L., and strawberry guava, *P. cattleianum* Sabine, are often referred to as the “guava belt” (Vargas et al. 1983a). The D₂ zone is primarily native forest. Pertinent information on elevation, rainfall, and ecosystem type for each of these vegetation zones is summarized in Fig. 1.

**Survey Procedure.** Male presence in an area was determined from fruit fly traps baited with trimedlure (Vargas et al. 1983a) placed in trees or shrubs at eye level along transects at 1.5 - 3.0 km intervals. When host plants were found in vegetation zones, traps were placed on them. Some traps were established along roadways; however, most were placed along jeep trails and footpaths (Fig. 1). Equal numbers of traps were placed in dry and wet habitats. Traps were serviced at monthly intervals from November 1985 to October 1986.
FIGURE 1. (Upper) Map of west Oahu, showing the major vegetation zones and some habitat characteristics. (Lower) Map of west Oahu, showing the location of traps, indicated by numbers, and spatial distribution of C. capitata based on trap and fruit infestation data.
Female presence in an area was determined from host fruits collected near traps. Procedures for rearing pupae from infested fruits are described in Vargas et al. (1983a). Numbers of C. capitata adults that emerged from pupae obtained from various tests were recorded. In addition to C. capitata, oriental fruit fly, Dacus dorsalis Hendel, and parasitoids emerged from the fruit samples. In this paper only data on C. capitata are presented.

U.S. Dept. of the Interior Geological Survey maps and a planimeter were used to determined the areas occupied by C. capitata.

Statistics. Results were analyzed with the t test and General Linear Models programs of SAS Institute (1982).

RESULTS

Population Distribution Pattern. Fig. 1 summarizes distribution of C. capitata throughout west Oahu. The Makaha and Waianae Valleys were classified as the high density permanent areas. Five traps in this area caught 90.4% of the total flies captured during the study. Two areas along the Waianae and Mokuleia coasts were characterized as low density permanent habitats for C. capitata. Areas throughout the "guava belt" were classified as temporary habitats. No C. capitata were captured in high elevation native forests.

West Oahu comprises an area of 563 km². On the basis of this study we categorize 23 km² as C. capitata high density permanent residency areas, 143 km² low density permanent areas, 140 km² as temporary residency areas and 249 km² as uninhabited. These figures indicate that the high density area represented only about 4% of the total area.

Population Variation with Locality. From November 1985 to October 1986, 96.2% of the traps in xerotropical habitats and 61.5% of the traps in pluviotropical habitats caught flies. Mean capture rates (±SE) for traps placed in xerotropical habitats were significantly higher than for traps placed in pluviotropical habitats (1.38 ± 0.72 vs 0.04 ± 0.02 flies/trap/day) (t = -1.84; df = 25; P<0.08). Mean number of months (±SE) traps caught flies was 6.8 ± 0.8 in xerotropical habitats and 2.6 ± 0.7 in pluviotropical habitats (t = 3.9; df = 50; P<0.01). Highest capture rates were obtained from traps placed on coffee trees in Makaha (Fig. 1 left, trap no. 45 and 46) and Waianae (trap no. 40 and 41) Valleys. No C. capitata were captured in traps placed on native ohia, Metrosideros collina (Forst.) Gray, and koa, Acacia koa Gray, trees near the summit of Mt. Kaala (trap no. 14, 15, 16, and 17), on guava at certain localities throughout the windward guava belt (trap no. 11, 12, 22, and 29), and on ornamental kamani, Calophyllum inophyllum L., trees at Barber’s Pt. (trap no. 32). Mean capture rates (±SE) under host and nonhost trees were 0.97 ± 0.54 and 0.16 ± 0.10 flies/trap/day, respectively (t = 1.4; df = 42; P = 0.17).

Permanent and Temporary Residency. Number of months flies were captured in traps ranged from 0-12. Frequencies (y) for the number of months traps captured flies (x) were 11, 8, 6, 3, 2, 2, 0, 3, 4, 1, 3, 4 and 5 for 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11 and 12 months, respectively (N = 52 traps;
x = 4.7; SE = ± 0.6). A locality was categorized as a permanent residency site if flies were captured 7-12 months of the year and as a temporary residency site if flies were captured 1-6 months of the year.

**Population Dynamics in Permanent Residency Areas.** Permanent residency areas were divided into two groups, high population (> 1 fly/trap/day) and low population (< 1 fly/trap/day) areas. To graphically illustrate the concept of permanent and temporary residency, annual population fluctuations are presented for five traps in or near feral coffee stands in Makaha and Waianae Valleys, five traps in fruit trees in residential or farm properties near the Mokuleia Coast, and four traps in feral guava stands in the northern Waianae Mountains (Fig. 2). Data on *C. capitata* abundance for these three areas indicate tremendous differences. In high density permanent residency areas, mean numbers of flies (±SD) were highest (560 ± 286 flies/trap/month) in May and lowest (37 ± 23 flies/trap/month) in September. In low density permanent residency areas, numbers of *C. capitata* were highest in April (11 ± 6 flies/trap/month) and lowest (1 ± 0.6 flies/trap/month) in August. This habitation pattern was characteristic not only of the Mokuleia-Waialua-Poamoho area, but also of the large coastal residential area from Makaha to Nanakuli on the leeward side of the Waianae Mountains.

**Population Dynamics in Temporary Residency Areas.** In temporary residency areas *C. capitata* populations were extremely low. During 7 months of the year no flies were caught in these areas. Peak captures occurred in September (2 ± 3 flies/trap/month). In general, this habitation pattern was characteristic not only of the northern Waianae Mountain area but also of the “guava belt” throughout the Waianae Mountains. For all traps placed throughout the “guava belt” the relationship between the total number of flies captured (y) and the number of months in which there was a positive trap catch (x), expressed as a quadratic equation (y = 0.004x^2 - 0.023x + 0.036; R^2 = 0.96), indicated that the total flies captured increased with the total number of months flies were captured per year. Traps with highest capture rates were closest to the high density permanent residency area in Makaha and Waianae Valleys. Furthermore, numbers of *C. capitata* were high in temporary residency areas when they were low in permanent residency areas.

**Host Plant Distribution.** *C. capitata* host plants can be classified into two categories: feral and nonferal. Feral hosts are those that are not cultivated and are growing naturally in towns, valleys and on hillsides. Nonferal hosts are those that are cultivated in residential areas or on farms. The major feral host plants observed in west Oahu were coffee, *Coffea arabica* L., common guava, and strawberry guava. Coffee was present only in upper areas of Makaha and Waianae Valleys. Common guava occurred as thick patches and isolated plants throughout gulches and upland areas of the Waianae Mountains and Wahiawa area. Strawberry guava was present in thick patches from 300-1000 m elevations throughout the Waianae Mountain Range as well as near the town of Wahiawa. Generally, strawberry guava and common guava occurred throughout the C and D1 zones (Fig. 1). The
FIGURE 2. Residency type and seasonal occurrence of *C. capitata*, as indicated by mean number of *C. capitata* caught per sample date. (A) Waianae and Makaha Valleys; (B) Mokuleia coast, Waialua and Poamoho; (C) North Waianae Mountains. Bars represent months when ripe fruits were present.
major nonferal host plants observed in west Oahu were mock orange, *Murraya exotica* L.; false kamani, *Terminalia catappa* L.; mango, *Mangifera indica* L.; and citrus, *Citrus* spp. These plants were in residential areas, parks, farms and roadsides. Many cultivated host plants were sparsely distributed throughout inhabited areas of Mokuleia, Makaha, Waianae, Nanakuli, and Barber's Pt. No host plants were found in pineapple fields of Kunia, Wahiawa, and Poamoho and in sugarcane fields of Ewa and Wai'alua.

**Host Plant Phenology.** In west Oahu fruiting cycles vary in wild areas as well as in residential areas. For example, in wild areas in the southern Waianae Range near Palehua, strawberry guava fruited during April to May. However, in the northern Waianae Range on the slopes of Mt. Kaala, it fruited from May to October. Coffee season began in December and ended in April of the following year. Common guava fruited from June to November. In residential areas mango, false kamani and mock orange fruited during specific months. Other fruits, such as different varieties of citrus, fruited throughout the year. In general, although there were seasonal fruiting patterns in certain fruits (Fig. 2), there were host fruits in various quantities throughout the year. Hence, *C. capitata* breeds throughout the year in west Oahu.

**Production of Host Fruits.** Fruit samples collected during November 1985 to October 1986 showed that coffee produced the highest number of flies. Coffee from Makaha Valley produced as many as 234 flies per kg of fruit (Table 1). In general, other host fruits produced low numbers of flies. These data are in agreement with trap data which showed *C. capitata* populations high in coffee areas and low in other areas. However, the coffee areas are relatively small as compared to other hosts like common guava and strawberry guava.

**DISCUSSION**

**Application of Findings to SIRM.** The sterile insect release method (SIRM) of eradication of *C. capitata* in Hawaii needs to be developed from a historical community ecology perspective. Releases of sterile flies should be based on distribution and population behavior of wild flies. Nishida et al. (1985) have suggested that the present loci of *C. capitata* distribution are fragments of a much broader original niche. One eradication strategy suggested by this study is to use sterile flies to change further the *C. capitata* habitation pattern. The sequence of procedures would be to 1) change high density permanent *C. capitata* residency to low density permanent residency; 2) change low density permanent residency to temporary residency islandwide; and 3) force *C. capitata* to extinction islandwide by use of eradication treatments. In the case of west Oahu the highest number of sterile flies needs to be directed at the small 22 km² high density area in Waianae and Makaha Valleys. The second largest number of sterile flies would be used to convert low density permanent habitats to temporary habitats. In the case of west Oahu this includes the 143 km² Mokuleia and Waianae coastal areas. The remaining sterile flies need to be released over the 140 km² area of *C. capitata* temporary residency. There is no need to
**TABLE 1.** Fruit collection data during November 1985-October 1986 from host plants near traps, showing number of collections, total fruits collected and number of tephritid fruit fly pupae and adults of *C. capitata* recovered.

<table>
<thead>
<tr>
<th>Date</th>
<th>Locality</th>
<th>Species</th>
<th>No. of collections</th>
<th>Total No. collected</th>
<th>No. of pupae</th>
<th>No. of adults</th>
<th>No. of adults/kg</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Waianae Coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11/20</td>
<td>Makua</td>
<td>False kainani</td>
<td>1</td>
<td>158</td>
<td>162</td>
<td>18</td>
<td>5.7</td>
</tr>
<tr>
<td>1/13, 2/27</td>
<td>Makaha</td>
<td>Coffee</td>
<td>3</td>
<td>6180</td>
<td>2061</td>
<td>1445</td>
<td>233.8</td>
</tr>
<tr>
<td>3/12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3/21, 4/19</td>
<td>Waianae</td>
<td>Coffee</td>
<td>2</td>
<td>3002</td>
<td>279</td>
<td>60</td>
<td>20.0</td>
</tr>
<tr>
<td>2/12</td>
<td>Makaha</td>
<td>Mock orange</td>
<td>1</td>
<td>1599</td>
<td>7</td>
<td>5</td>
<td>8.0</td>
</tr>
<tr>
<td>6/10</td>
<td>Makaha</td>
<td>Mango</td>
<td>1</td>
<td>54</td>
<td>202</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>6/10, 8/12</td>
<td>Kaena</td>
<td>Guava</td>
<td>4</td>
<td>523</td>
<td>985</td>
<td>21</td>
<td>53.0</td>
</tr>
<tr>
<td>10/3, 10/27</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mokuleia Coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11/20, 11/27, 1/8, 8/6, 9/18, 10/15</td>
<td>Mokuleia</td>
<td>False kainani</td>
<td>6</td>
<td>950</td>
<td>2546</td>
<td>19</td>
<td>1.4</td>
</tr>
<tr>
<td>3/23</td>
<td>Poamoho</td>
<td>Orange</td>
<td>1</td>
<td>11</td>
<td>6</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>11/23</td>
<td>Poamoho</td>
<td>Tangerine</td>
<td>1</td>
<td>20</td>
<td>9</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>5/16, 6/13</td>
<td>Poamoho</td>
<td>Jabon</td>
<td>5</td>
<td>122</td>
<td>810</td>
<td>14</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>7/9, 9/18, 10/15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9/18</td>
<td>Waianahua</td>
<td>Tangelo</td>
<td>1</td>
<td>12</td>
<td>38</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>N. Waianae Mts.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5/16, 6/3</td>
<td>Mokuleia Uplands</td>
<td>Guava</td>
<td>2</td>
<td>166</td>
<td>1126</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td>5/14, 10/22</td>
<td>Kaala</td>
<td>Guava</td>
<td>2</td>
<td>154</td>
<td>1027</td>
<td>7</td>
<td>0.8</td>
</tr>
<tr>
<td>5/14, 7/23</td>
<td>Kaala</td>
<td>Strawberry guava</td>
<td>3</td>
<td>833</td>
<td>1180</td>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td><strong>S. Waianae Mts.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2/5</td>
<td>Palehua</td>
<td>Guava</td>
<td>1</td>
<td>32</td>
<td>51</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>4/25, 5/14</td>
<td>Palehua</td>
<td>Strawberry guava</td>
<td>2</td>
<td>433</td>
<td>321</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>5/16, 6/19</td>
<td>Kunia</td>
<td>Guava</td>
<td>2</td>
<td>90</td>
<td>376</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>9/18</td>
<td>Schofield Barracks</td>
<td>Strawberry guava</td>
<td>1</td>
<td>291</td>
<td>12</td>
<td>1</td>
<td>0.5</td>
</tr>
</tbody>
</table>
release sterile insects in native forests or sugarcane and pineapple fields since C. capitata are not present in these areas.

Generally, the permanent/temporary residency classification scheme for C. capitata eradication can be applied to all the major islands in Hawaii. For example, on the island of Kauai high density permanent residency areas include only the Waimea Canyon complex and Hanapepe Valley (Vargas et al. 1983a). Low density permanent residency areas include the entire west coast from Poipu to Polihale, as well as the mountain recreation areas of Kokee.

Sterilized C. capitata adults show a low propensity to disperse (Wong et al. 1982, Cunningham and Couey 1986). Consequently, sterile flies need to be released in or as close as possible to the distribution centers. Most C. capitata permanent breeding areas in west Oahu are small and accessible by paved or dirt roads. Ground releases would place sterile flies closest to the distribution centers. Temporary breeding areas of west Oahu are large and inaccessible by ground. Therefore, release of sterile insects in these areas would have to be from aircraft.

A potentially useful observation was made in this study about temporary residency. Total number of flies captured is clearly related to the number of months flies are captured. Therefore, once the habitation pattern has been reduced to temporary residency over the entire island, the additional effort required in an area to eradicate the fly will be determined by the total number of months wild flies are captured.

Eradication of C. capitata must precede eradication of D. dorsalis. The present study is further evidence of the previously documented suppressive effect of D. dorsalis on C. capitata (Bess 1953, Keiser et al. 1974). It was evident that large numbers of C. capitata were recovered from coffee where D. dorsalis was scarce, but few C. capitata were recovered from guava where D. dorsalis was common. The tremendous buildups of D. dorsalis in guava are also well documented (Newell and Haramoto 1968; Vargas et al. 1983b). Nishida et al. (1985) have discussed displacement of C. capitata by D. dorsalis throughout most of the Hawaiian Islands, except in certain localized areas. We postulate that additional eradication pressure from man through such methods as the release of sterile flies will complement competitive pressure from D. dorsalis and drive C. capitata to extinction in areas such as the "guava belt". Furthermore, parasitoids attacking D. dorsalis also attack C. capitata. For these reasons it would be only logical to eradicate C. capitata from Hawaii before eradicating D. dorsalis. If the reverse strategy is chosen, there will be the danger of C. capitata moving into niches vacated by D. dorsalis.

Although experimental applications of SIRM previously have resulted in various levels of suppression (Steiner et al. 1962, Harris et al. 1986, and Wong et al. 1986), C. capitata has never been eradicated from any island in Hawaii probably because of lack of isolation to prevent immigration of wild flies into the target areas. Presently, strategies are being developed for a SIRM pilot test to eradicate C. capitata from Kauai. The present study provides distributional information whereby sterile flies can be most effectively and efficiently utilized.
Ecology of C. capitata Distribution. Previous reports on west Oahu (Harris and Lee 1986) imply that C. capitata is present only in Makaha and Waianae Valleys and nearby residential areas. Results of the present study indicate that C. capitata infests fruits in four of five major vegetation zones of west Oahu and occurs over a wider area than previously reported. Trap and fruit infestation data clearly indicate that C. capitata occurs most frequently in xerotropical leeward areas (A and B zones) and the loci of distribution are coffee stands located in the Makaha and Waianae Valleys. These findings are similar to earlier observations we made in coffee stands in Waimea Canyon and Hanapepe Valley on the western side of the island of Kauai (Vargas et al. 1983a). The present report is the first documented evidence of C. capitata distribution throughout windward areas of the Waianae Mountains and along the Mokuleia coast of Oahu.

In the Kauai study, we did not fully recognize two important distributional characteristics of C. capitata evident from this study. First, there was a wide range of C. capitata permanent residency throughout xerotropical coastal habitats (A and B zones). In west Oahu this included the Waianae and Mokuleia coasts, ca. 40km of coastline where residential backyard host fruits and common ornamental trees in parks provided year round breeding sites for C. capitata. Secondly, there was a widespread occurrence of C. capitata throughout guava areas when coffee was not in season. Previously, we associated temporary residency with fruiting of localized stands of strawberry guava near high density C. capitata areas (Vargas et al. 1983a). In the present study we recognized that coffee and guava have distinctly different fruiting seasons. Although guava was only lightly infested, its presence throughout the extensive “guava belt” greatly increases the range of C. capitata throughout west Oahu.

We speculate that C. capitata populations increase with the fruiting of coffee in Makaha and Waianae Valleys. When ripe coffee is no longer available (May-November), portions of the population migrate into nearby residential and upland guava areas. However, in these areas competition for resources is severe due to the presence of large numbers of D. dorsalis. This may be the factor that keeps C. capitata numbers low and variable.

We view residency patterns as indicators of the suitability of the environment to C. capitata. Obviously, in favorable environments there will be permanent populations. However, in areas where conditions are periodically favorable and unfavorable, residency becomes temporary. Factors related to favorable and unfavorable environments are not clearly understood. However, trap and fruit infestation data in this study clearly indicated that one important factor is host fruit phenology. We observed that an abundance of ripening host fruits in an area resulted in positive trap catches. However, we noticed that fruiting of nonhost fruits (sea grape, Coccoloba uvifera (L.) Jacq.) and flowers that produce nectar (plumeria, Plumeria acuminata Ait.) also influenced the temporary and permanent residency phenomenon. Traps under shrubs with ripe nonhost fruits and flowers frequently captured flies. Feeding of fruit flies on ripe nonhost fruits and nectar has been discussed by Nishida (1980).
ACKNOWLEDGMENTS

We wish to thank Grant U'chida for processing of fruits. We also thank Jim Carey (Dept. of Entomology, Univ. of California, Davis), Frank Chang (Dept. of Entomology, Univ. of Hawaii, Honolulu) and Asher Ota (Hawaiian Sugar Planters Association, Aiea, HI) for critical reviews of this manuscript.

REFERENCES CITED


