

**Contributions to the Biology and Ecology of the
Oriental Fruit Fly, *Dacus dorsalis* Hendel
(Diptera: Tephritidae), in Hawaii**

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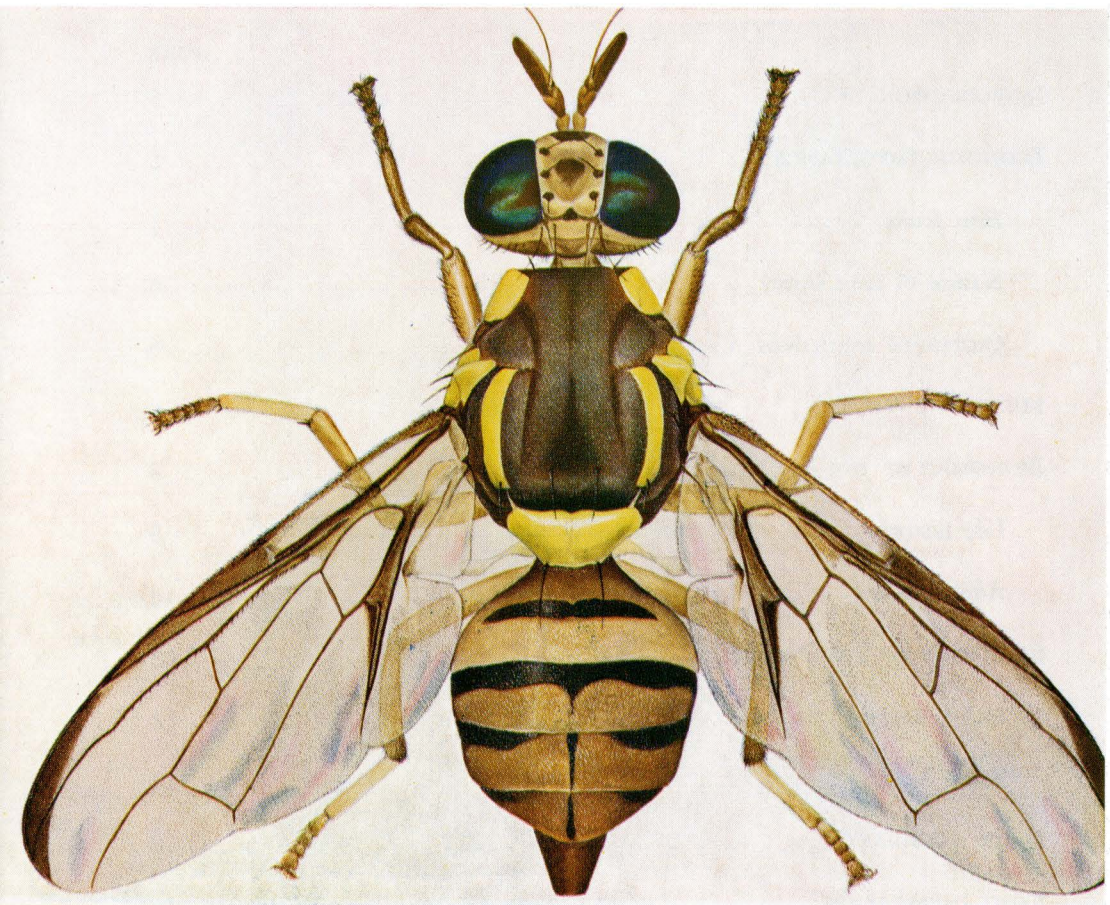
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Female of *Dacus dorsalis* Hendel. Life size about 9 mm. long.

Contributions to the Biology and Ecology of the Oriental Fruit Fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae), in Hawaii

Henry A. Bess and Frank H. Haramoto

The Oriental fruit fly, *Dacus dorsalis* Hendel, was first found in Hawaii in 1945 (van Zwaluwenburg, 1947). During the following year it increased to epidemic populations and caused serious damage to many crops throughout the Hawaiian Islands. Prompt action was taken to combat this pest through the introduction of biological control agents. Explorations were made in many countries and several entomophagous insects of fruit flies were subsequently introduced into Hawaii.

A study of the establishment and spread of the introduced entomophagous insects and the assessment of their importance in reducing the abundance of *D. dorsalis* was one of the aspects of the extensive cooperative program which was assigned to the entomologists of the Hawaii Agricultural Experiment Station. Some of the information obtained on the progress and status of the fly and parasites from 1948 to 1955 has been discussed in earlier papers (Bess, van den Bosch, and Haramoto, 1950; van den Bosch, Bess, and Haramoto, 1951; Bess and Haramoto, 1958*a*). However, the studies on the status of the fly and parasites were continued through 1959 and several aspects of their biology and ecology have been investigated which were not covered in the earlier papers. The purpose of this paper is to present the biology, ecology, and status of *D. dorsalis* and its principal parasites and to evaluate the role of entomophagous insects that prey upon it.

ECONOMIC IMPORTANCE

During the peak years (1947-50) of *D. dorsalis* abundance in Hawaii, the intensity of attack by this fly on many fruits was so great that often no salable or edible fruits were harvested. Furthermore, quarantine restrictions prevented the shipment of untreated fresh fruits and flowers to the mainland United States. These necessary quarantine restrictions have created a great hindrance to the development of export markets for Hawaiian produce.

(1) Host fruits

More than 120 species of fruits served as hosts of *D. dorsalis* during the peak years of abundance. Some of these fruits were of minor importance as hosts but the following ones were often heavily infested and produced large numbers of

flies: avocado, *Persea americana* Mill.; ball kamani, *Calophyllum inophyllum* L.; bananas, *Musa* spp.; coffee, *Coffea arabica* L.; false kamani, *Terminalia catappa* L.; guava, *Psidium guajava* L.; mango, *Mangifera indica* L.; mock orange, *Murraya exotica* L.; mountain apple, *Eugenia malaccensis* L.; papaya, *Carica papaya* L.; peach, *Prunus persica* (L.) Batsch.; rose apple, *Eugenia jambos* L.; strawberry guava, *Psidium cattleianum* Sabine; and Surinam cherry, *Eugenia uniflora* L. These species grow on all of the major islands and may be abundant locally in habitats favorable to them.

(2) Nature of fruit injury

The injury caused by *D. dorsalis* to fruits is similar to that caused by the melon fly, *Dacus cucurbitae* Coquillett, and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The surface defect resulting from an ovipositional puncture may be increased by sap oozing from it, discoloration, or from abnormal growth around it (fig. 1*a, b, d*). The puncture may also provide an entrance for various decay organisms which hasten the breakdown of the injured fruits. When young fruits of some species are stung, such as those of passion fruit, *Passiflora edulis* f. *flavicarpa* Degener, they become malformed (fig. 1*b*) and usually drop off the vines prematurely. These forementioned types of injuries are often considerable in such fruits as passion fruit and litchi although very few individuals survive in them. Maggots, as such, are objectionable and their feeding and tunneling reduce the attractiveness of the flesh for human consumption (fig. 1*c*). When abundant, the maggots may even devour a large portion of the fruit. In feeding, the maggots make holes in the surface which provide entry for additional organisms, such as drosophilids and nitidulids, resulting in further fermentation and decomposition of the fruits.

(3) Quarantine restrictions

The direct and indirect costs and losses that may be attributable to the establishment and enforcement of the necessary quarantine regulations to prevent *D. dorsalis* entry into the mainland United States cannot be determined but may be much greater than the direct damage to the fruit crops. In a sense, these precautionary restrictions impose a trade barrier and certainly curtail the expansion and development of export markets for some Hawaiian crops. Commodity treatment has helped to alleviate this to some extent; however, the added costs and the possible reduction in quality due to the treatments place our potential export crops in an unfavorable position to compete successfully with similar products from other areas.

METHODS

Studies were begun in the fall of 1948 to follow the abundance and damage by *D. dorsalis* and the progress of the parasites. These studies were later expanded to include periodic sampling on most of the islands from 1950 through 1959. Since the bionomics of the fly and of the various parasites were important to the population studies, these were investigated concurrently.

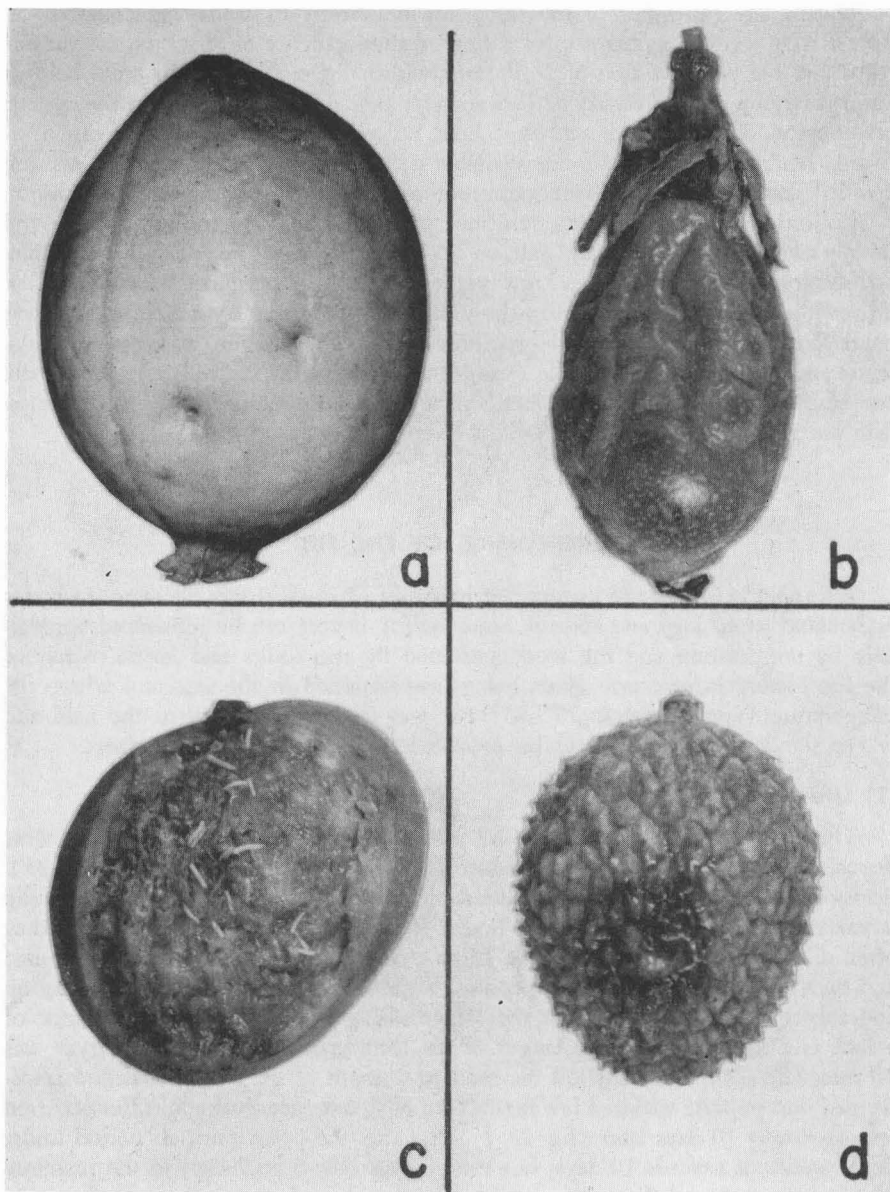


FIGURE 1. Fruits damaged by the Oriental fruit fly. *a*, guava with oviposition punctures; *b*, passion fruit with gall-like growth and shriveling due to oviposition; *c*, mango, showing larvae and damaged tissues; *d*, litchi, showing discoloration around oviposition puncture.

During the early part of the study a wide variety of fruits was collected on the different islands to obtain information on the incidence of attack on the various fruits and the parasitization of *D. dorsalis* within them. These fruits were held in an insectary on the University of Hawaii campus in Honolulu to obtain the desired information. Since guava is a favored host, occurs on thousands of acres of uncultivated land, and some fruits are available at all seasons, it was used for making detailed comparative studies of variations associated with localities and seasons.

Collections of guavas from established plots were made monthly on Oahu and usually twice a year, spring and fall, on the islands of Hawaii, Kauai, Lanai, Maui, and Molokai. During the first few years each collection normally consisted of 20 or more ripe fruits but during the past 3 years the size of the collections was reduced to 10 fruits. The usual procedure was to remove the maggots from the fruits and rear them in a suitable medium as described by Newell, van den Bosch, and Haramoto (1951). Further details in regard to the methods used in obtaining data are given later in the respective sections.

BIONOMICS OF THE FLY

Information on the life history and habits of *D. dorsalis* was necessary to better understand its ecology and control. Since its life history can be influenced appreciably by temperature and the food consumed by the adults and larvae, much of the life history information given below was obtained in the insectary where the temperature (approximately 75°–85° F.) was less variable than in the field and where standardized diets could be provided for the adults and maggots.

(1) Life history

The elliptical white eggs, about 1.2 mm. in length and .2 mm. in width, were deposited in batches 3–15 approximately $\frac{1}{4}$ inch inside host fruits (fig. 2*b*). Eclosion took place some 30–36 hours after deposition and the active young larvae remained nearby for several hours. Later as the larvae fed and grew they often dispersed throughout the fruit. Most larvae finished feeding in about 7 days and then left the fruit or rearing medium. Such larvae have the habit of curling up and subsequently springing into the air, resulting in dispersal for a distance of a foot at a time. The average length of the fully grown creamy-white larvae was 10 mm. (fig. 2*c*). They entered the sand to a depth of $\frac{1}{2}$ to 2 inches and transformed into puparia within a few hours (fig. 2*d*). Emergence of adult flies occurred approximately 10 days later (fig. 2*e*, *f*). Probably the preoviposition period under field conditions exceeds 10 days; however, it was only 5 to 7 days in the insectary when newly emerged flies were provided with a diet of sugar, water, and protein hydrolysate. The greater portion of the eggs deposited was laid during the first 3 weeks after emergence but some females lived and produced eggs for 2 months. Therefore, the length of time required from egg to egg in the insectary was about 25 days but without doubt this was less than that normally required under field conditions.

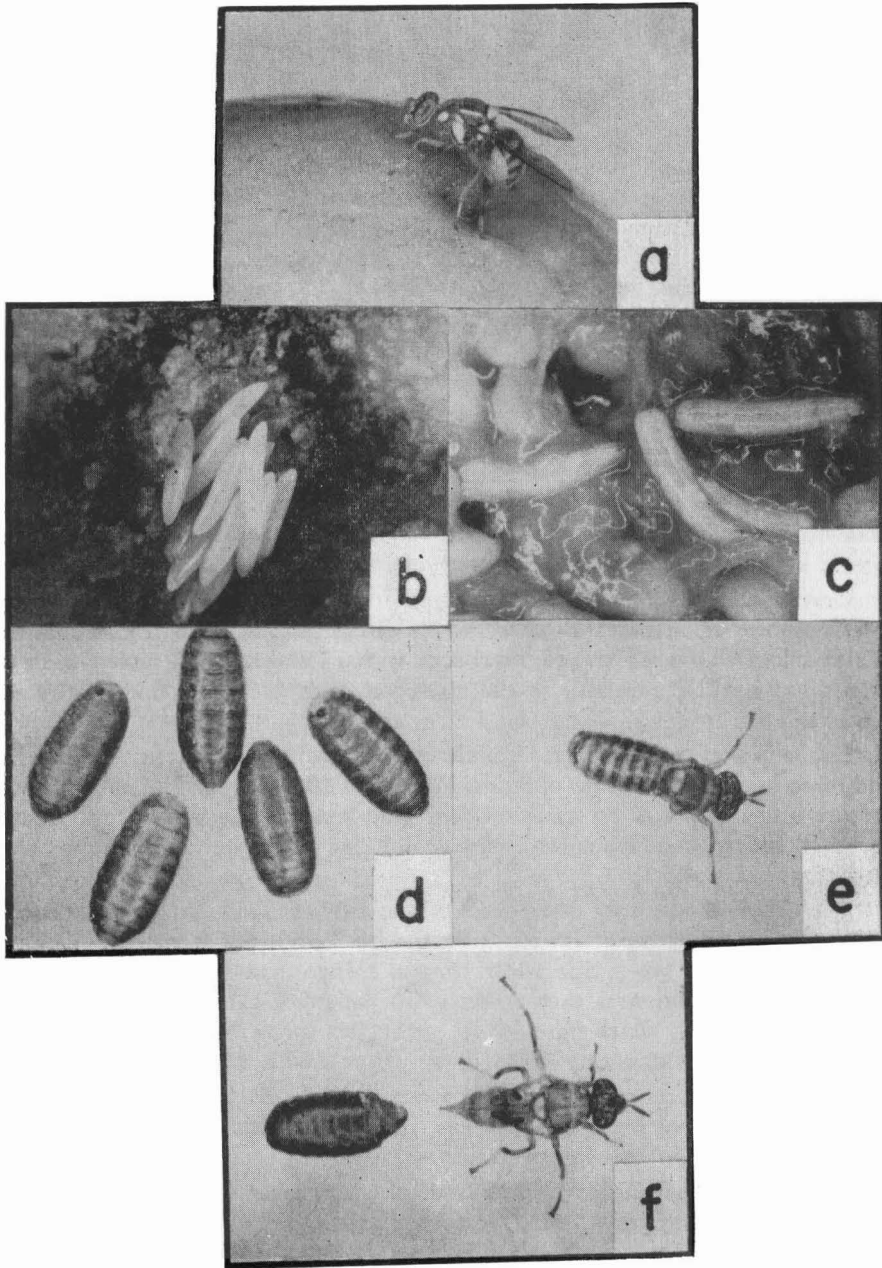


FIGURE 2. Life cycle of the Oriental fruit fly. *a*, fly ovipositing in old puncture; *b*, eggs *in situ* in guava; *c*, third instar larvae within guava; *d*, puparia; *e*, adult partially emerged from puparium; *f*, newly emerged fly.

(2) Adult habits

Many of the habits of *D. dorsalis* are similar to those of other tephritids (Boyce, 1934; Christenson and Foote, 1960; Lathrop and Nickels, 1932; Nishida and Bess, 1957; Bess and Haramoto, 1958*b*), some of which have an important influence on fly abundance and control.

Emergence of the flies usually occurred between 8:00–10:00 A.M. The newly emerged flies remained relatively inactive for about an hour, during which time the wings were expanded and the body color darkened. Soon thereafter, they became active and fed. Hagen (1950) found sugar, water, and protein hydrolysate to be an excellent diet for *D. dorsalis*, as well as for *D. cucurbitae* and *C. capitata*. Flies in the field were seen feeding on a variety of materials, such as extrafloral glandular secretions (Nishida, 1958), nectar, honey-dew, damaged ripe or decomposing fruits, and animal feces which no doubt have many of the nutrients present in the above standardized diet.

The first mating was observed on the fifth day, or 4½ days after emergence. Around dusk in the evenings the males made high-pitched buzzing sounds which were followed by copulation. A pair remained in copulation 2 to 5 minutes. Both males and females commonly mated several times; however, females isolated after a single mating laid fertile eggs throughout their life span.

Gravid females were induced to oviposit in the insectary at all hours during the day; however, in the field there was a distinct periodicity in oviposition. At Waimanalo, Oahu, where ovipositional activity was followed for 3 successive days, oviposition occurred primarily in the afternoon, with a peak around 3:00–4:00 P.M. (table 1).

Common sites of oviposition were old ovipositional punctures (fig. 2*a*), cracks, and other injuries in the skin of fruits. More than 100 eggs were often deposited in such sites. This was especially evident with mangoes in which eggs tended to be concentrated in fruits with surface injuries, while uninjured fruits were often not infested.

The degree of maturity or ripeness of the different fruits had a pronounced effect on their attractiveness to attack by the fly. Passion fruits were not vulnerable to oviposition when ripe while banana, mango, and papaya became more attractive to oviposition as they ripened. On the other hand, passion fruit was most susceptible to attack when very green and guava when "mature-green" rather than when either very green or very ripe (table 1).

Varietal differences in susceptibility to attack by *D. dorsalis* were pronounced with certain kinds of fruits. For example, the Pirie variety of mango was more heavily infested than the Haden variety.

Adults of *D. dorsalis* move in and out of guava areas freely. Flies were not found in numbers on guava fruits and foliage except during the peak oviposition hours in the afternoons (table 1). Food and shelter are apparently obtained from plants other than guava. In fact, in 1948 and 1949 thousands of flies were observed "resting" on panax (*Nothopanax guilfoylei* (Cogniaux and Marchal) Merrill) hedges, which is not a host. Males congregate on certain species of

TABLE 1. Numbers of *D. dorsalis* and parasites on mature-green, semi-ripe, and ripe guava fruits (20 of each kind) at different hours of the day (February 21, 22, and 23, 1953)

RIPENESS OF FRUIT AND INSECT SPECIES	TIME OF OBSERVATION														TOTAL NUMBERS	
	6 AM	7	8	9	10	11	12 NOON	1	2	3	4	5	6 PM			
Mature-green																
<i>D. dorsalis</i>	0	0	0	0	0	3	3	13	18	24	23	10	2	96		
<i>O. longicaudatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>O. vandenboschi</i>	0	0	0	1	0	1	0	0	0	0	0	0	0	2		
<i>O. oophilus</i>	0	9	14	9	14	19	13	5	9	18	24	15	12	161		
Semi-ripe																
<i>D. dorsalis</i>	0	0	0	0	1	2	5	5	10	10	10	2	0	45		
<i>O. longicaudatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>O. vandenboschi</i>	0	0	1	2	2	1	0	3	2	2	1	1	1	16		
<i>O. oophilus</i>	1	4	8	13	15	13	6	11	9	11	10	7	6	114		
Ripe																
<i>D. dorsalis</i>	0	0	0	0	0	1	0	4	2	6	4	0	0	17		
<i>O. longicaudatus</i>	0	0	3	0	0	0	2	2	1	3	1	7	0	19		
<i>O. vandenboschi</i>	0	0	1	1	2	0	0	1	2	2	2	2	0	13		
<i>O. oophilus</i>	0	1	3	1	3	1	0	1	1	0	0	0	0	11		

plants, such as mokihana, *Pelea anisata* Mann, but males and females may be equally abundant on other plants. For example, 162 males and 168 females were counted on passion fruit vines at Waimanalo on July 6, 1957.

BIONOMICS OF THE PARASITES

The life histories of the parasites were similar in many respects but some of their habits were distinctly different and these probably played an important role in their success as control agents. The opiine species introduced may be classified into 3 general groups according to their ovipositional habits: (1) the *longicaudatus* group, (2) the *vandenboschi* group, and (3) the *oophilus* group. Females of the first group oviposit in larger (second and third instar) larvae, those in the second in smaller (first instar) larvae, and those of the third in the eggs of their hosts. Species belonging to groups 1 and 2 are known as larval parasites, while those in the third group are referred to as egg-larval parasites. The bionomics of a species representative of each of the groups are presented in some detail below.

(1) Life histories

Opius longicaudatus (Ashmead)

The spindle-shaped hymenopteriform egg of *O. longicaudatus* when fully developed in the uterus measures .40–.45 mm. in length and .08–.09 mm. in diameter at the widest point (fig. 3a). After deposition it swells, practically doubling in width prior to hatching. The eggs were primarily deposited in large larvae but occasionally eggs were laid in small larvae. From rearing records it was found that this parasite was better adapted to large larvae than to small ones (Bess, van den Bosch, and Haramoto, 1950). At the time of hatching the first instar larva is heavily sclerotized in the head region and has sac-like appendages on the ventral anterior margin of the first thoracic segment (fig. 3c). Molting into the second instar was delayed until after the host larva formed a puparium. After the puparium was formed the *O. longicaudatus* larva developed rapidly and the adult emerged some 18 days after the egg was laid.

The body of the adult *O. longicaudatus*¹ is ochraceous with variable amounts of black bands on the dorsum of the abdomen. The length of the body varied between 3.5–5.0 mm. and the ovipositor between 4.0–5.5 mm. This species was easily reared and the adults lived for many weeks in the insectary. Most of the introduced opiines belonged to the *longicaudatus* group.

Opius vandenboschi Fullaway

The glabrous club-shaped egg of *O. vandenboschi* is approximately .70 mm. in length and .10 mm. in width. Prior to hatching it increases in width but not

¹ Four varieties of *O. longicaudatus* have been described by Fullaway (1953). Practically all of the specimens reared in these studies were of the variety *malaiensis* and the information presented here was obtained with that variety.

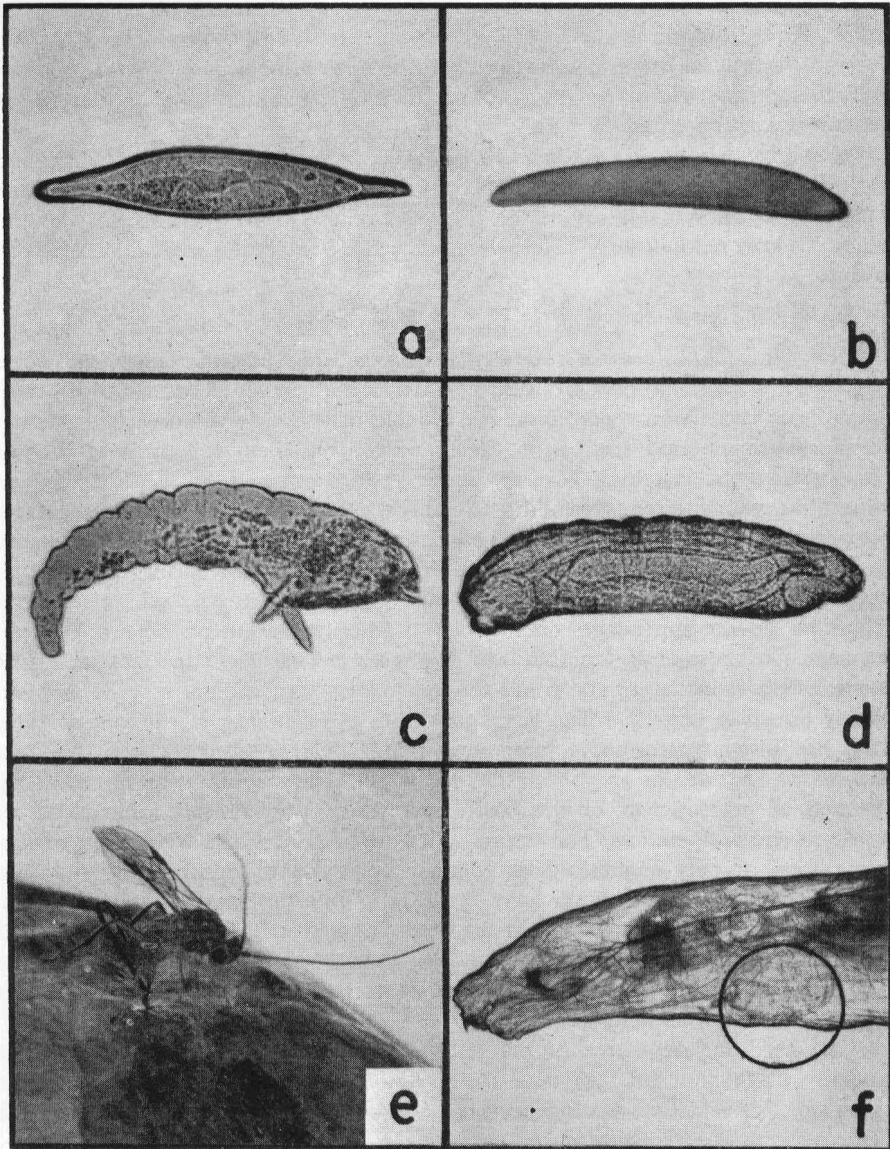


FIGURE 3. Parasites of the Oriental fruit fly. *a*, mature uterine egg of *O. longicaudatus*; *b*, mature uterine egg of *O. oophilus*; *c*, first instar larva of *O. longicaudatus*; *d*, first instar larva of *O. oophilus*; *e*, adult of *O. longicaudatus* ovipositing in infested guava; *f*, first instar *O. oophilus* larva (encircled) within body cavity of first instar *D. dorsalis* larva.

to the extent as the egg of *O. longicaudatus*. Eggs are deposited in small host larvae. After hatching the first instar larva, which is similar to that of *O. oophilus*, does not molt until the host larva forms a puparium. About 7 days were required for development within the puparium, with an elapsed time of approximately 18 days from egg to adult.

The body length of *O. vandenboschi* females varied from 3.5–4.0 mm. and the ovipositor from 2.5–3.5 mm. The body of the female is predominantly black with the posterior two-thirds of the abdomen yellowish brown. The body of the males is also predominantly black, except for the venter of the abdomen, which is tan.

Opius oophilus Fullaway

The hymenopteriform egg of *O. oophilus* is glabrous and translucent white (fig. 3*b*). When deposited it measures .30–.36 mm. in length and .06–.07 mm. in diameter at the widest point, but may double in width by the time of hatching. The incubation period was 28–35 hours, which was about the same as that of *D. dorsalis* eggs. Hatching occurred either before eclosion of the host egg or within the young larva, depending upon the age of the host egg at the time the parasite egg was deposited. With its sharp sickle-shaped mandibles the young *O. oophilus* larva cut a transverse slit along the cephalic end of the egg through which it escaped. The first instar larva does not have a heavily sclerotized head region or sac-like appendages on the ventral anterior margin of the first thoracic segment, like those of *O. longicaudatus* (fig. 3*c, d*). The first is the most active of the 4 instars. It moves around freely through the body cavity and may be oriented in any direction (fig. 3*f*). The larva grew slowly, remaining in the first stadium until the host larva formed a puparium. Immediately prior to molting the larva was about 1.0 mm. in length, .3 mm. in width. The stadium was governed by the rate of development of the host larva, which was, in turn, influenced by nutrition and temperature. The second, third, and fourth stadia were brief, requiring a total of only about 7 days. Immediately prior to transforming into the prepupal stage the fourth instar larva was 3.2–3.7 mm. in length and 1.6–1.8 mm. in width. About 1 day was spent in the prepupal stage and 5–8 days in the pupal stage. Males emerged 1 to 2 days earlier than females. The duration of the combined egg, larval, prepupal, and pupal stages was 18–20 days, or about 2 days longer than that of its host.

The head and prothorax of the adult are ochraceous, while the abdomen is basically black and the legs tan. The body length was 3.5–4.0 mm. and the ovipositor 3.0–3.5 mm. Mating occurred within a day after emergence and the first eggs were laid on the third day.

(2) Adult habits

Some of the general habits, such as time of emergence, feeding, and mating, were essentially the same for the different parasites studied. It is irrelevant to repeat these general habits for all species.

Emergence of *O. oophilus* was found to be influenced by temperature. In the field emergence occurred between 8:00 A.M. and 12:00 noon; however, in the insectary it was induced at all hours of the day through temperature regulation. The young adults began feeding soon after emergence. Adults provided with honey and water in droplets lived 25–30 days while those that were given no food died within 24 hours after emergence. In the field adults were repeatedly observed feeding at various hours of the day on scale-infested foliage where honey-dew was prevalent.

Males of *O. oophilus* exhibited mating behavior soon after emergence but females were not receptive during the first few hours. Both males and females mated more than once.

As indicated above, there are striking differences among the 3 principal parasites, *O. longicaudatus*, *O. vandenboschi*, and *O. oophilus*, from the standpoint of their ovipositional habits. The female of *O. oophilus* oviposited in both viable and nonviable eggs of *D. dorsalis*. Once the ovipositor was inserted into the oviposition puncture of the fly, several eggs were laid before complete removal of the ovipositor from the puncture. Often all eggs within a group of eggs at an oviposition site received 1 or more *O. oophilus* eggs. However, where eggs were exposed to individual *O. oophilus* females in cages there was very little superparasitization. Five caged females began laying eggs on the third day after emergence and laid 3,703 eggs over a period of 34 days. Following death the 5 females were dissected and found to contain a total of 104 eggs in their ovaries. In the field *O. oophilus* females, unlike *D. dorsalis* females, oviposited during the greater part of the daylight hours without any distinct peak in ovipositional activity (table 1). Females were especially active during sunny calm days, while when there was strong wind or rain they remained inactive on the lower surfaces of leaves and fruits. As indicated earlier, newly laid *D. dorsalis* eggs were more abundant in mature-green guava fruits than in ripe ones, and *O. oophilus* females also occurred in greater abundance on mature-green than on ripe guava fruits (table 1). *O. oophilus* females were seldom observed on ground fruits even though *D. dorsalis* females were present and ovipositing in fallen fruits.

The female of *O. vandenboschi* inserted her ovipositor directly through the epidermis of the fruit rather than through the *D. dorsalis* ovipositional puncture, as in the case of *O. oophilus*. At the time of attack the larvae were still in the vicinity of the hatched eggs in the puncture. Females frequented the semi-ripe and ripe fruits on the trees which contained predominantly host larvae in a suitable stage for attack. Although young host larvae were present in ground fruits, adults of this parasite, like those of *O. oophilus*, were seldom seen on ground fruits.

O. longicaudatus females were commonly associated with over-ripe fruits which contained large *D. dorsalis* larvae (fig. 3e). The large larvae are well dispersed in such fruits, rather than being localized as in the case of eggs and newly hatched larvae. Therefore, in large fleshy fruits, such as guavas, peaches, and mangoes, many larvae may be some distance from the surface and beyond the reach of the ovipositor. Although females of *O. longicaudatus* were seen ovipositing in

ripe fruits on trees, they were more abundant on fallen fruits, many of which were in an advanced stage of decomposition.

Parasitization by a particular species was usually higher in certain fruits than in others, indicating some degree of fruit preference. For example, parasitization by *O. longicaudatus* was conspicuously higher in kamani, mango, peach, and mock orange fruits than in other fruits. Furthermore, since this parasite has become scarce, it has been easier to obtain it from those fruits than from guavas. On the other hand, parasitization of *D. dorsalis* by *O. oophilus* has been less in mangoes than in guavas and parasitization by *O. vandenboschi* has been less in guavas than in kamani and mock orange fruits.

FRUIT ABUNDANCE

Since the fly population is dependent upon host fruits suitable for the development of the maggots, fruit abundance was investigated along with other factors that might influence abundance of the fly and parasites. Guavas have apparently been the principal host fruit of the fly in Hawaii; however, many others (see page 5) have contributed to the over-all population, especially during the peak years (1947-50). Guavas grow where there is sufficient rainfall from sea level to around 3,500 feet elevation but do not grow in areas where there is less than about 20 inches of annual rainfall (Hosaka and Thistle, 1954). Despite the availability of some guava fruits throughout the year, there is a peak in the fruiting season which may extend over a period of 4-6 months in some areas and only a few weeks in others. These differences are apparently associated with the distribution and total rainfall but other factors may also be involved.

The fruiting season of guava was studied for a number of consecutive years in plots at several distantly located areas on Oahu. A scale of 0 to 8 was used to estimate the fruit abundance in the individual plots as follows: 1, approximately 10 ripe fruits within a radius of 50 feet of the center of a plot; 2, when approximately 20 fruits; 3, when approximately 40 fruits; and increasing geometrically in a similar manner. The results obtained for 3 consecutive years in 3 plots at each of 5 distantly located areas are shown in figure 4, lower graph. Fruits were abundant from July to January and relatively scarce from February to June, with distinctly fewer fruits in the early spring. Fruits within a specific locality were absent as long as 4 consecutive months and were also more abundant one year than another (fig. 4, upper graph).

The fruiting periods of the different host fruits of *D. dorsalis*, which still occasionally contribute many flies, vary year to year but generally they are as follows: mango, rose apple, and mountain apple in summer; kamani and coffee in the fall; and mock orange in the winter. This means that appreciable quantities of host fruits other than guava are available to *D. dorsalis* at all seasons.

FRUIT INFESTATION

Fruit infestation data are unavailable for the period prior to December 1948. However, from all reports of entomologists and laymen, infestation and damage

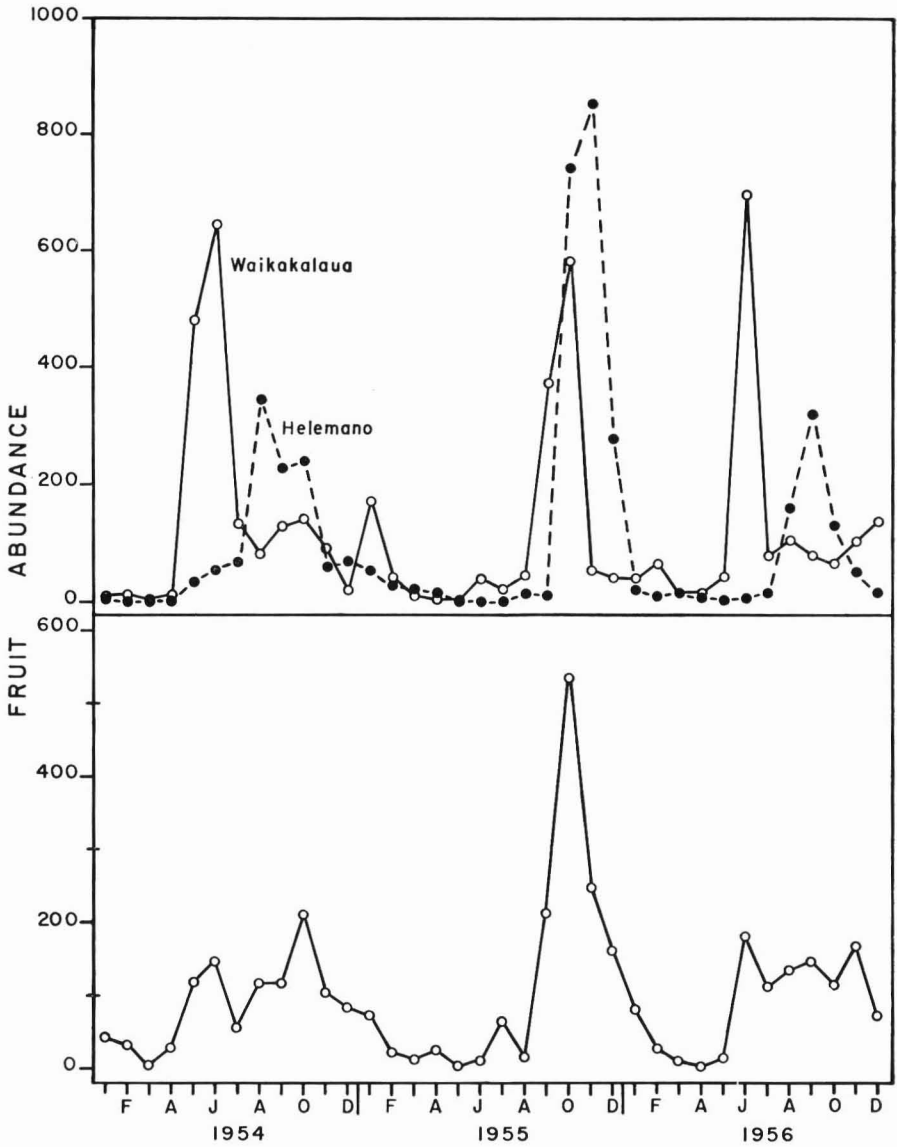


FIGURE 4. Seasonal variations in guava fruit abundance; lower graph, number of fruits per plot at 5 localities; upper graph, number of fruits per plot in 2 localities.

were much greater during 1947 and 1948 than in subsequent years. A number of fruit collections were made between December 1948 and November 1949 but the total number of larvae within them was not determined since during this period the objective sought was to determine the hosts of the fly and the success of the parasites from the standpoint of establishment, build-up, and spread. In several of the guava collections made during this period all fruits were infested and the larval count exceeded 50 per fruit even though many of the larvae were not recovered. For example, 44 guavas collected at Poamoho, Oahu, on September 9, 1949, contained 5,457 *D. dorsalis* larvae, or an average of 124 larvae per fruit.

TABLE 2. Summary of the data obtained from the guava collections showing numbers of fruits, flies,¹ and parasites involved

NUMBERS	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
OAHU										
Total fruits	10,589	7,724	5,506	2,579	2,218	2,008	2,228	904		
Fruits with larvae		2,746	2,016							
Flies	18,399	2,921	3,402	3,729	2,062	1,075	2,892	1,202		
Parasites	24,511	5,341	7,789	7,763	5,186	2,480	5,412	3,276		
HAWAII										
Total fruits	1,423	1,406	710	220	200	442	280		204	628
Fruits with larvae	892	866	301	148	137	198	48		102	285
Flies	3,827	2,908	605	454	409	245	46		1,303	1,301
Parasites	2,657	4,804	854	430	428	448	75		972	602
MAUI										
Total fruits	2,364	1,076	540		80	135			147	350
Fruits with larvae	1,307	659	192		74	47			69	149
Flies	5,627	819	163		194	90			441	673
Parasites	2,136	1,527	366		136	144			445	649
KAUAI										
Total fruits	236	190	48						110	75
Fruits with larvae		146	31						89	50
Flies	654	752	82						693	262
Parasites	501	614	94						484	263
LANAI										
Total fruits	254	85	120	100	40	120			40	80
Fruits with larvae	196	31	63	58	13	110			11	18
Flies	1,114	8	136	95	35	632			51	58
Parasites	333	29	81	171	3	69			0	42
MOLOKAI										
Total fruits	172	266	80			87		16		
Fruits with larvae	138	149	42			75		4		
Flies	709	251	23			271		0		
Parasites	143	324	78			371		0		

¹ Except for the Lanai and Molokai collections, *D. dorsalis* made up more than 99 percent of the flies reared. However, *C. capitata* usually outnumbered *D. dorsalis* in the Lanai collections, and also made up an appreciable portion of those reared from the Molokai collections.

All of the fruits were infested and 9 of them contained more than 200 larvae each. By November 1949, it had become apparent from the numerous parasites recovered from the fruit collections and the widespread occurrence of adult parasites in the field that intensive collecting of fruits to study the role of the parasites in the control of *D. dorsalis* could be started without fear of hazard to the parasites. Guava, for the reasons given above, was selected as the standard fruit to be used in these quantitative investigations. In November systematic collecting of guavas at monthly intervals was begun in a number of plots on Oahu and continued through 1956, with similar collections in March, June, September, and December of 1957. In addition, guava fruits were collected periodically from 1950 through 1959 at several localities on Hawaii, Maui, Lanai, Molokai, and Kauai (table 2).

Although *D. dorsalis* is a multivoltine species, there were distinct seasonal trends in fruit infestation and adult abundance. The seasonal fluctuations shown in figure 5 are representative of those that have occurred during the past decade. Each year the maximum infestation occurred some time between April to September and the minimum between November to March (table 3). The infestation in December of 1949 was about 3 times as great as the next highest minimum infestation present during the 9 consecutive winters for which infestation data

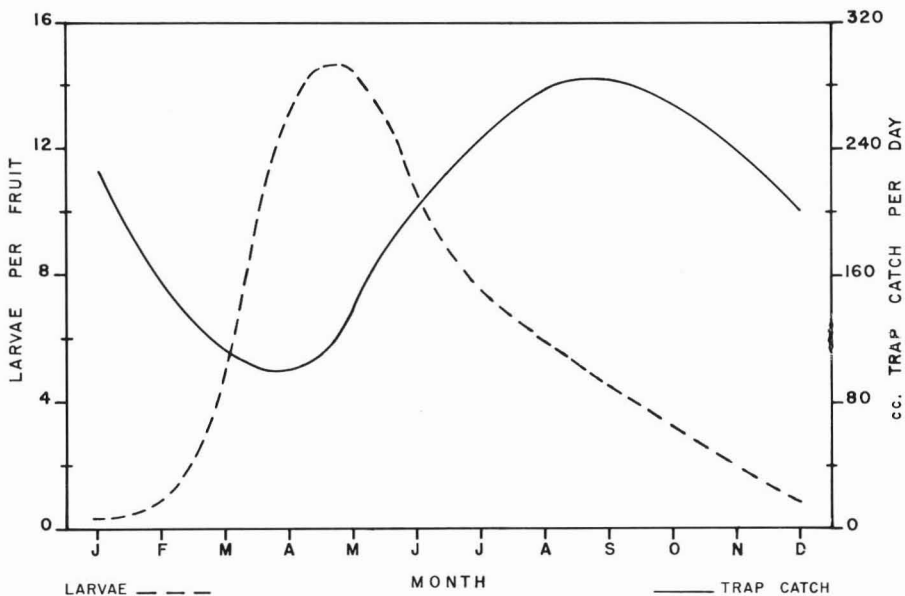


FIGURE 5. Fruit infestation and trap catches (adult males) on Oahu for 1956.

TABLE 3. Fruit fly larvae per fruit in guavas collected on Oahu, 1949-1957

MONTH	YEAR									MEAN
	1949	1950	1951	1952	1953	1954	1955	1956	1957	
January		4.1	0.4	0.8	1.7	2.1	1.0	0.4		1.1 ± 0.3
February		5.1	2.4	4.4	3.2	3.6	1.3	0.8		2.6 ± 0.6
March		9.0	1.7	3.0	4.5	4.3	1.3	4.4	4.7	3.4 ± 0.5
April		15.0	2.1	1.9	5.7	6.9	4.1	14.7		5.9 ± 1.9
May		22.9	5.9	2.7	6.5	4.5	4.4	14.3		6.4 ± 1.7
June		18.4	4.0	4.8	7.9	6.1	4.2	5.4	9.5	6.0 ± 0.6
July		7.8	5.1	4.7	15.4	6.2	3.5	7.2		7.1 ± 0.5
August		4.9	3.5	10.1	23.8	4.0	3.0	4.5		7.7 ± 2.9
September		8.4	2.8	4.4	7.0	5.6	4.9	6.2	4.9	5.5 ± 0.6
October		4.5	1.2	1.2	2.9	3.7	1.9	2.9		2.6 ± 0.2
November	13.3	1.1	1.0	0.6	2.2	3.6	0.7	2.1		1.6 ± 0.1
December	7.1	0.4	1.5	0.4	1.5	1.3	0.4	0.9	0.6	0.9 ± 0.2
Mean		4.5 ± 1.3 ¹	2.6 ± 0.5	3.3 ± 0.8	6.9 ± 1.9	4.3 ± 0.5	2.6 ± 0.5	5.3 ± 0.4	4.9 ± 1.8	

¹ From July 1948 to July 1950 was the period of establishment, build-up, and spread. Therefore, only the data obtained after the latter date were used in calculating the means.

are available, but in the preceding winters of 1947 and 1948 it was no doubt far greater than in 1949.

As late as 1949 adults of *D. dorsalis* were so numerous that they commonly entered buildings in numbers and oviposited in fruits in grocery stores and roadside fruit stands. Although less abundant in 1950 than in 1949, the trap catch of adult males for 1950 was 4 to 5 times that for subsequent years (table 4). During July of 1950 the estimated number of adult males caught per day exceeded 30,000 for the 11 traps, or a total of over 900,000 flies during the month.

TABLE 4. Data on guava infestation and trap catches of male flies on Oahu

	1949 ¹	1950	1951	1952	1953	1954	1955	1956
	<i>Larvae per fruit (monthly)</i>							
Maximum	—	22.9	5.9	10.1	23.8	6.9	4.9	14.7
Minimum	7.1	0.1	0.1	0.4	1.5	1.3	0.4	0.9
Mean for year		8.5	2.6	3.3	6.9	4.3	2.6	5.3
	<i>Total catch (cc) in 11 traps per day per month²</i>							
Maximum		1,640	395	362	393	322	358	308
Minimum		269	143	93	146	77	20	83
Mean for year		940	227	232	245	220	145	202

¹ Only data for November and December available.

² Trapping begun in July 1950.

The *D. dorsalis* population and fruit infestation continued to decline until 1951 but there was no further reduction through 1956 when the regular fruit collections were discontinued on Oahu. During the 6-year period, 1951-56, the yearly means of the infestation fluctuated within narrow limits, 3-7 larvae per fruit. In 1957 guavas were collected within the Oahu plots at 3-month intervals and the infestation data obtained indicated that the larval infestation for 1957 was within the range of the infestation for the preceding 6-year period.

The infestation by *D. dorsalis* was consistently higher in certain localities than others. The higher infestations in guavas commonly occurred in relatively warm humid areas at elevations below 500 feet and the lower infestations occurred in relatively cool situations above 1,000 feet on the leeward side of mountains. Infestation data based on the number of eggs per fruit obtained on Oahu (table 5)

TABLE 5. *D. dorsalis* infestation based on eggs in guava fruits from Oahu plots in 1957

MONTH	NUMBER FRUITS	PERCENT WITH EGGS	NUMBER EGGS/FRUIT
March	212	71	20
June	224	76	38
September	240	80	26
December	220	64	10

in 1957 from 3 or more plots at each of 2 localities characteristic of each of these types were as follows:

	March	June	September	December
Tantalus (cool)	0	7	2	1
Helemano (cool)	8	7	3	0
Waikakalaua (warm)	13	66	15	15
Kahaluu (warm)	30	61	38	26

On the other islands relatively high infestation occurred in the Kalapana area on Hawaii, Kipahulu area on Maui, and the Puhī and Hanalei areas on Kauai, while relatively low infestation occurred in the Kona area on Hawaii, Kula area on Maui, and Lawai area on Kauai. On the islands of Lanai and Molokai, most guavas collected were from about 500 feet elevation where it was cool. The infestation on both islands was low like that in similar situations on the other islands.

CONTROL

Biological control had been successful in combating several insect pests in Hawaii and this approach to the *D. dorsalis* problem received major emphasis by the authors. Exploration for parasites and predators of *D. dorsalis* was begun

promptly following its establishment. Explorers were sent to many countries and intensive search made in those regions where *D. dorsalis* was known to occur (Clancy, Marucci, and Dresner, 1952). Of the several entomophagous insect species introduced, all were hymenopterous parasites, except one, which was a predaceous staphilinid beetle, *Thyreocephalus albertisi* (Fauvel). This beetle and most of the parasites have not become important. However, 3 of the parasites, *O. longicaudatus*, *O. vandenboschi*, and *O. oophilus*, became abundant following their establishment and each played an important role in the reduction of the *D. dorsalis* populations. Many individuals of *O. incisus* were also reared but the species was never abundant. In addition, a few individuals of the following species were recovered from field fruits infested with *D. dorsalis*: *Dirbinus giffardii* Silvestri, *Syntomosphyrum indicum* Silvestri, *Spalangia philippinensis* Fullaway, *Tetrastichus giffardianus* Silvestri, and *Tetrastichus dacicida* Silvestri.

Some of the pertinent information concerning the history of the succession of each of the 3 principal parasites following their liberation, 1947 to 1951, although discussed elsewhere (van den Bosch, Bess, and Haramoto, 1951; Bess, van den Bosch, and Haramoto, 1961), is given here as background material for the discussion that follows. Since *O. longicaudatus* was easily reared in the insectary and was liberated in large numbers in 1948 it was given the advantage of early establishment and an opportunity to increase on the large *D. dorsalis* populations present. During the spring and summer of 1949 it was the predominant parasite, with approximately 20 percent of the many thousands of *D. dorsalis* larvae in the Oahu fruit collections parasitized by this species. In a few collections parasitization by *O. longicaudatus* exceeded 50 percent. By fall *O. vandenboschi* had succeeded *O. longicaudatus* in predominance and during the period between October 1949 and July 1950 the monthly average parasitization by *O. vandenboschi* on Oahu varied between 25 and 35 percent and in individual collections parasitization exceeded 75 percent. In July *O. oophilus* succeeded *O. vandenboschi* as the predominant parasite and over 95 percent of the many thousands of parasites reared from the Oahu guava collections during the past 9 years, 1951–1959, have been *O. oophilus*. However, in the Puna area on Hawaii periodically fairly large numbers of *O. vandenboschi* have been obtained. As late as May of 1958 a total of 279 *O. vandenboschi* adults, representing 28 percent parasitization, were reared from guavas collected at 5 localities in Puna. Elsewhere only an occasional specimen of this opiine has been obtained from the numerous guavas collected since 1953. The scarcity of all of the parasites other than *O. oophilus* in recent years is illustrated by the data given in table 6.

The over-all parasitization of *D. dorsalis* in guava fruits on Oahu rapidly increased during 1949 and 1950 and the mean for the last 6 months of 1950 was slightly above 75 percent, which was as high as the mean for the following 7 years. The yearly means from 1951 through 1956 fluctuated within relatively narrow limits (table 7). The minimum monthly means shown in table 7 usually occurred in March, which indicated some seasonal effects.

The history of parasite succession and rates of parasitization on the other islands were similar to those of Oahu.

TABLE 6. Numbers of the different species of parasites reared from guavas in different years

ISLAND	NUMBER OF ADULT PARASITES			
	<i>O. longicaudatus</i>	<i>O. vandenboschi</i>	<i>O. incisi</i>	<i>O. oophilus</i>
	1950			
Oahu ¹	1,841	8,185	30	11,962
Hawaii	258	2,199	4	158
Maui	622	1,231	0	189
Kauai	69	429	3	0
Lanai	40	300	0	0
Molokai	0	120	0	3
	1956			
Oahu	2	0	6	4,764
	1958			
Hawaii	0	279 ²	0	636
Maui	0	5	0	413
Kauai	0	0	0	450

¹ April–December collections only; *O. vandenboschi* and *O. oophilus* not reported separately for January–March collections.

² All of these parasites were obtained from 5 localities in the Puna region.

TABLE 7. Percent parasitization of fruit fly larvae in guava fruits collected on Oahu, 1949–1957

	1949	1950 ¹	1951	1952	1953	1954	1955	1956	1957	MEAN
January		49	91	85	78	79	82	74		82 ± 3
February		42	72	61	72	77	65	76		72 ± 3
March		41	69	53	64	81	48	57	56	61 ± 4
April		48	69	79	66	51	64	40		62 ± 6
May		40	81	81	70	61	71	64		71 ± 4
June		48	78	71	79	73	60	67	81	73 ± 3
July		73	81	83	68	83	84	77		78 ± 2
August		78	79	69	57	75	65	72		71 ± 3
September		73	85	69	76	70	73	63	72	73 ± 2
October		68	80	79	75	74	76	75		75 ± 2
November	37	77	71	73	70	71	67	66		71 ± 1
December	44	83	92	74	69	66	52	81	90	76 ± 5
Mean		75 ± 2	79 ± 2	73 ± 3	70 ± 2	72 ± 3	67 ± 3	68 ± 3	75 ± 7	

¹ From July 1948 to July 1950 was the period of establishment, build-up, and spread. Therefore, only the data obtained after the latter date were used in calculating the means.

There were often large variations in parasitization at a locality from one collection date to another, as well as among different localities on a specific collection date. It may be well to point out some of the more obvious factors that might account for these variations. The exposure period of *D. dorsalis* eggs to

O. oophilus females was less than 48 hours and a considerable number of these hours were at night when there was little or no ovipositional activity by *O. oophilus*. Parasite oviposition was also curtailed by inclement weather, especially rain and high wind. Furthermore, *D. dorsalis* eggs are usually deposited in batches of several eggs and if *O. oophilus* females fail to contact an oviposition site the entire batch will be missed. Fruit and *D. dorsalis* abundance may also have influenced parasitization and contributed to the variations in parasitization between dates and localities. It would require many intensive and extensive data to determine differences in the efficiency of the parasite under the various ecological conditions in Hawaii. Despite the many factors involved that influenced the fly and parasites, parasitization has been high on all of the islands since 1951.

There are many organisms that influence directly and indirectly the abundance of *D. dorsalis* but major alterations of the natural environments would be necessary to obtain detailed data on the influence of organisms such as predators. Nevertheless, during this lengthy study many observations were made on the activities of several species which caused mortality during the different stages of the fly.

Competitors, such as birds and rodents, often eliminated large numbers of *D. dorsalis* eggs and larvae by consuming them along with the fruit. These animals often ate practically all fruits within an area when fruits were scarce. In an experiment conducted in a forested area composed predominantly of guava trees with no fruits on them, a number of guava fruits were hung from branches and by the following day 25 of the 54 fruits exposed had been partially or completely eaten by birds. In localized areas, the African snail, *Achatina fulica* Bowdich, consumed many fruits. Certain insects, such as drosophilids and nitidulids, fed within the same fruits with *D. dorsalis* larvae but they offered little competition for food since there was no evidence of starvation of *D. dorsalis* larvae. Two other tephritids, *D. cucurbitae* and *C. capitata*, may co-exist and compete with *D. dorsalis* for food in individual fruits but in nature each of these 3 species tends to predominate in certain fruits and in certain localities (Bess, 1953). However, these various insects were involved in the mechanical transmission of microorganisms which caused the rapid fermentation and decomposition of fruits, resulting in the media becoming unsuitable for the development of the *D. dorsalis* larvae.

In several instances ants, especially *Pheidole megacephala* (Fabricius), were observed destroying *D. dorsalis* eggs, larvae, and adults. In fact, in the insectary during the warmer months entire cultures of *D. dorsalis* have been eliminated when barriers against ants were not provided. Under field conditions predation by ants was conspicuously higher during the summer months and in the drier, hotter areas. Jumping spiders were frequently observed feeding on *D. dorsalis* adults but they probably had little influence on the abundance of this species. Earwigs and staphylinids were commonly seen in numbers under fallen fruits. Marucci (1955) observed individuals of 2 species of earwigs, *Anisolabis eteronoma* Borelli and *Sphingolabis hawaiiensis* (Bormans), feeding on *D. dorsalis* maggots in the field and also reared both species on *D. dorsalis* maggots in the laboratory. Due to the polyphagous nature of predators, and since eggs and maggots

TABLE 8. Egg mortality and larval parasitization data obtained from guavas¹ collected quarterly at each of 4 localities on Oahu in 1957

	MARCH	JUNE	SEPTEMBER	DECEMBER
Number of eggs	780	1,920	1,151	408
Percent nonhatch	51	72	78	94
Number of larvae	355	545	177	22
Percent of larvae parasitized	46	83	68	100

¹ Four fruits were collected from each of 3 plots at each locality on each collection date. Therefore, each of the above figures is based on the information obtained from 48 fruits.

of *D. dorsalis* consumed by predators were usually parasitized in excess of 50 percent, the value of the predators has been questioned.

Microorganisms were an important group of the natural enemies of *D. dorsalis*. A number of species were observed associated with mortality in the different stages but critical studies of their pathology were not made. In several instances adults became infected with *Nosema* sp. (Hagen, 1952) and *Beauveria bassiana* (Balsamo) Vuillemin in the insectary but no morbidity or mortality caused by these organisms was encountered in the field. On the other hand, the bacterium, *Serratia marcescens* Bizio, and 2 fungi, *Penicillium* sp. and *Aspergillus* sp., were closely associated with the high mortality of *D. dorsalis* eggs and parasitization by *O. oophilus* under some ecological conditions. To gain more specific information about the interrelationships of these organisms and *O. oophilus* several different studies were made both in the insectary and field. The data obtained from a series of quarterly guava collections of 12 fruits at each of 4 localities on Oahu—Helemano, Kahaluu, Manoa, and Waikakalaua—revealed that mortality from microorganisms varied with season and locality, as well as with intensity of parasitization by *O. oophilus* (table 8). The punctures made in the chorions by ovipositing females apparently served as avenues of entry for the organisms, for experimentally they did not penetrate undamaged eggs. The close interrelationship between the microorganisms and *O. oophilus* in causing egg mortality is indicated by the information summarized below:

(1) low hatch was associated with high parasitization and high incidence of microorganisms within the nonhatched eggs;

(2) presence of mandibles of *O. oophilus* larvae in nonhatched infected eggs was directly proportional to the mortality;

(3) the microorganisms were isolated and cultured from the ovipositors of field-collected *O. oophilus*;

(4) low hatch of *D. dorsalis* eggs when exposed to field-collected *O. oophilus* females and high hatch of those unexposed;

(5) high hatch of *D. dorsalis* eggs parasitized by insectary-reared *O. oophilus*;

(6) high hatch of unparasitized *D. dorsalis* eggs placed in oviposition punctures with heavy fungus growth; and

(7) high differential mortality between eggs with chorions punctured with fungus-contaminated spicules in contrast to those punctured with aseptic spicules.

Much work has been done on the chemical control of *D. dorsalis* in Hawaii by other workers. For information to this approach to the *D. dorsalis* problem the reader is referred to papers by Steiner (1952*a, b*), Steiner and Hinman (1952), and Tamashiro and Sherman (1955).

DISCUSSION

The high *D. dorsalis* population during the period when the parasites were being released and the presence of all the developmental stages of the fly throughout the year, no doubt enhanced the establishment of the parasites. The species that subsequently proved to be important were parasites of *D. dorsalis* in Southeast Asia, rather than of other tephritid species. Many of the introduced parasites were not obtained from *D. dorsalis* and possibly were not adapted for development in this species. Some of the parasites were probably handicapped due to interaction with other species of parasites which prevented their development. It was found that *O. oophilus* larvae prevented the development of *O. longicaudatus* and *O. vandenboschi* larvae when they occurred together in the same *D. dorsalis* maggot (van den Bosch and Haramoto, 1953). It was also subsequently found that *O. oophilus* prevented the development of *O. incisi* larvae (Haramoto, 1953). With such interspecific interaction the sequence in which the parasites were released could have been important to their establishment. The ready establishment and rapid build-up of the population of the 3 species which had an important effect on *D. dorsalis* lends support to the many known cases where introduced parasites, which subsequently proved effective in the control of their hosts, became readily established and soon demonstrated their effectiveness (Clausen, 1951).

Since *D. dorsalis* is dependent upon the abundance of host fruits for the production of its progeny, fruit abundance greatly influenced the fly population. There are several kinds of host fruits present throughout the year but there are more fruits in certain seasons and in some localities than in others. In some guava areas there were no fruits for several weeks while in others fruits were collected monthly for over 12 consecutive months. These variations in fruiting season probably influenced the incidence and intensity of infestation by *D. dorsalis*. In addition, environmental factors, such as temperature, precipitation, and wind, directly and indirectly affected the fly population and in certain localities the populations were consistently lower than in others. For example, at the higher elevations at Kula, Maui; Kona, Hawaii; and on Lanai; which are climatically similar, *D. dorsalis* has been relatively scarce. The infestation by it was also less during the winter months than at other months (fig. 6). These results indicate that this fly is not particularly well adapted to our cooler climatic situations, even though many suitable fruits are available in them. The retention of flies in specific areas, and the movement of flies into and out of them, also have an appreciable effect on *D. dorsalis* abundance and infestation.

The abundance of the parasites was in turn influenced by the populations of their hosts, which were, as indicated above, influenced by the fruit population

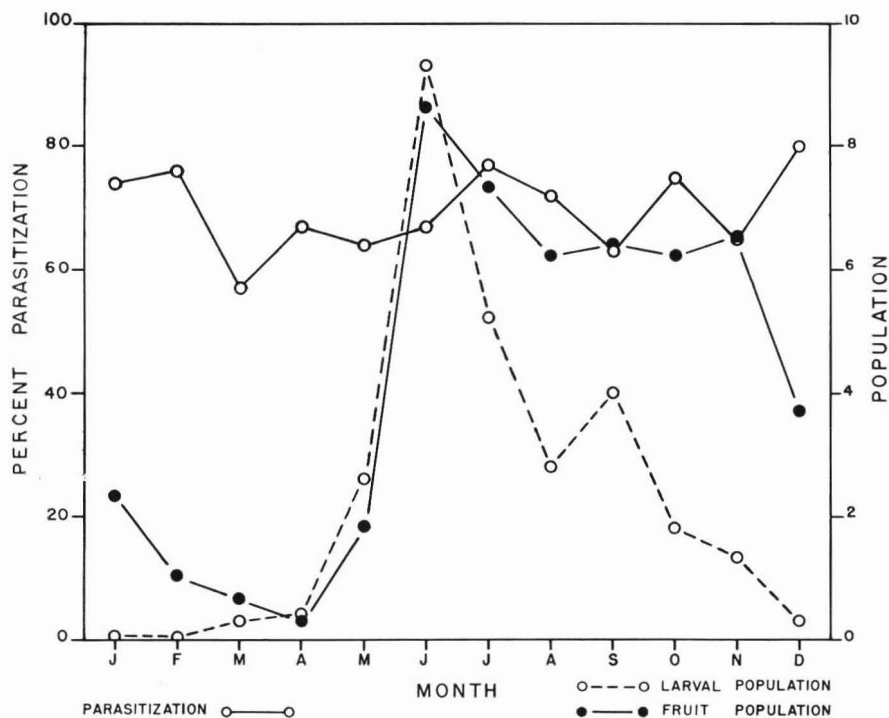


FIGURE 6. Fruit population, *D. dorsalis* larval population, and parasitization by *O. oophilus* within the Oahu plots during 1956. Population scale at right-hand side of figure; fruit, N × 1,000; larval, N × 10,000.

and a number of other factors. Parasitization tended to be persistently higher in certain localities than in others, and during the winter than in the spring. In many individual collections, parasitization was above 95 percent and in others less than 50 percent. The importance of these differences may be more fully appreciated if viewed in terms of the survival population at the different percentages of parasitization. At the 95 percent level there would be 1 fly surviving for every 19 being killed, while at the 50 percent level there would be 1 surviving for each 1 being killed. Furthermore, in the ensuing generation there would be 19 parasites available to attack the eggs laid by each surviving fly at the 95 percent level while only 1 parasite at the 50 percent level. The fluctuations in the populations of the fly and the parasites, and their great mobility, as well as the diverse fluctuating ecological conditions, make it extremely difficult to evaluate the role played by parasites in localized areas. The over-all abundance of the parasites fluctuated with that of *D. dorsalis*, with the percentages of parasitization remaining remarkably stable throughout the year (fig. 6) and throughout the past

decade (table 7). Since *D. dorsalis* populations were subsequently reduced to only a small fraction of what they were when the parasites were released, and since they have continued to destroy a large part of the populations during the past several years, there seems to be little doubt of the important role played by the parasites. There is a good likelihood that the parasites have exerted their maximum efficiency under present conditions and that they, especially *O. oophilus*, will continue to aid in the maintenance of the over-all *D. dorsalis* populations at relatively low levels.

SUMMARY

The investigations discussed in this paper were made primarily to follow the progress of the several parasites introduced to combat *Dacus dorsalis* Hendel and to assess their importance in Hawaii as biological control agents against this fly. However, in carrying out the studies pertinent information about the biology and habits of the fly and of the different parasites involved was needed in order to effectively make these studies, which were an integral part of the over-all cooperative program. The biologies and habits of the fly and of the 3 principal parasites are given, as well as the information obtained on the abundance and activities of the fly and parasites.

D. dorsalis became established in Hawaii in 1945, became exceedingly abundant, and caused much damage to fruit crops. Apparently the peak years of abundance were 1947 and 1948 but the fly continued to cause widespread damage during 1949 and 1950. During these years when it was especially abundant it was reared from over 120 different kinds of fruits and in large numbers from several of them. However, in recent years many of these fruits have been seldom infested. Many host fruits are available throughout the year; however, guavas serve as the principal medium in which the bulk of *D. dorsalis* populations develop.

Of the many entomophagous species introduced in this biological control program, only 3 species became abundant and played an important role in the reduction of the fly populations. The 3 parasites were *Opius longicaudatus* (Ashmead), *O. vandenboschi* Fullaway, and *O. oophilus* Fullaway, all of which developed successfully in both *D. dorsalis* and *Ceratitis capitata* (Wiedemann) but not in *Dacus cucurbitae* Coquillett. *O. oophilus* is the only 1 of the 3 parasites that has occurred in appreciable numbers since 1951. The history of parasitization is given in some detail, along with complementary data on fruit abundance, infestation, and related ecological aspects.

The great reduction in the abundance of *D. dorsalis* that occurred, along with the build-up of the populations of these parasites, indicated that the parasites played a major role in this reduction. Furthermore, *O. oophilus* has continued to parasitize a high percentage of the *D. dorsalis* egg population throughout the past 10 years and no doubt has been of key importance during this period in preventing the fly from increasing to higher populations and causing greater damage. Since 1951 there have been no noticeable over-all changes or improvements, and it appears that the maximum effects to be expected from *O. oophilus* and the other parasites have been realized.

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