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PLANT HOST SPECIFICITY AMONG FLOWER-FEEDING NEOTROPICAL DROSOPHILA (DIPTERA: DROSOPHILIDAE)*

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INTRODUCTION

Certain neotropical drosophilids both feed and breed in living flowers and are rarely or never collected by net sweeping over fallen plant parts, over fungi, or in fruit baited traps. Twelve of these species have been described recently by Pipkin (1964). They are distinct from two other aggregations of neotropical *Drosophilidae* species, the fungus-feeders and the ground-feeders, which sometimes breed in flowers (Pipkin, 1965a). For the present work the major collecting area was in forest at 2,500 feet on the mountain Cerro Campana, about 35 miles northwest of Panamá City, Panamá. The collecting area covered about 4 acres, including half an acre of coffee trees on cleared land. Sixty-four collections were made here throughout the year from July, 1960 to August, 1964. Fewer collections were made in central Panamá at the Ft. Sherman Reservation and at Madden Forest, Canal Zone; in western Panamá at El Volcán, Cerro Punta, Soná, and Almirante; in eastern Panamá at El Real; at Rio Raposo, Colombia (near Buenaventura) on the Pacific coast; at Leticia, Colombia, on the headwaters of the Amazon River; and at Trinidad, West Indies. Fig. 1 is a map showing these collection areas.

Among flower-feeding *Drosophila*, several species have been found associated with a single plant host. Others use two plant species, and still others feed and breed in flowers of several species. The purpose of this study is to present the evidence for plant host specificity among these flower dependent *Drosophila*, absence of it in others, and the bearing of this information on the evolutionary history of both drosophilid and host. Herbarium specimens and colored photographs of plants have been deposited in The National Museum of Costa Rica, San José, Costa Rica, and The U. S. National Museum, Washington, D. C.

METHODS

Adult flies were collected from flowers by aspiration and stored in vials containing moist laboratory culture medium. Flies were bred from flowers

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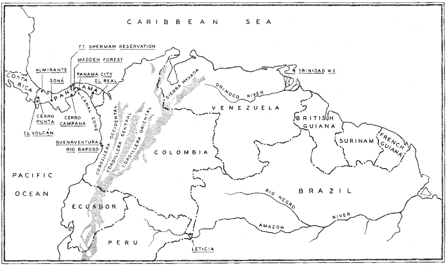

FIG. 1. Map showing collection areas.

broken off the plant. The drier flowers were put in quart mason jars; those with much sap, in flower pots with the drain hole plugged with cotton. When imagines hatched, cheese cloth covers replaced cotton stoppers of the containers. Vials containing culture medium were inserted into holes made in the covers. Hatching flies crawled into the collecting vials from time to time and were removed for examination.

RESULTS AND CONCLUSIONS

1. *Monophagous Drosophila*

Collections at the major study area at Cerro Campana proved that living flowers are used for larval and pupal development by both host specific and non-host specific flower-feeding *Drosophila* as well as by ground-feeding and fungus-feeding *Drosophila*. In this area a constant wet season occurs from May through December, intermittent rains falling to mid-January. Temperature varies from about 20 to 23 C throughout the year. The usual flowering periods of the plants occurring in sufficient numbers to support a *Drosophila* population are presented in Table 1. Here it is seen that four species, *D. nigrasplendens*, *D. hansoni*, *D. xanthopallescens*, and *D. mcclintockae* were bred each from flowers of a single plant species respectively; i.e., from *Heliconia subulata*, *Heliconia vellerigera*, *Calathea insignis*, and *Aphelandra micans*. Photographs of these plants which were growing side by side in thickets of the forested area appear in Fig. 2 (a–d). The four *Drosophila* species could be bred regularly from their respective hosts and never from the other plants listed in Table 1, even though two other species of *Heliconia* and two other species of *Calathea* were growing in the same plot intermingled with the plants supporting host specific

TABLE 1

Usual blossoming periods of forest plants at Cerro Campana, Panamá (2500 ft.) and *Drosophilidae* bred from their flowers.

Plant species	Usual period of blossoming	Flower-feeding *Drosophila* bred out	Ground-feeding *Drosophilidae* bred out	Fungus-feeding *Drosophilidae* bred out
Anthurium maximum	Jan., Feb.			
Impatiens sultani	Jan., Feb.			
Geonoma obvata	Jan., Feb.			
White hyacinth	Jan., Feb.		*Clastopteromyia* sp.	*Zygothrica* sp.
Cephaelis elata	Jan., Feb.			
Red mint	Jan. thru March			
Passiflora vitifolia	Feb., March			*Zygothrica* sp.
Crysophila warscewiczii	March, April			
Coffea arabica	April			
Siparuna nicaraguensis	April			
Heliconia subulata	Feb. thru Sept.	*D. nigrasplendens* *D. xiphiphora*		
Heliconia vellerigera	March thru Nov.	*D. hansoni* *D. xiphiphora*	*Clastopteromyia* sp.	
Cecropia mexicana	March thru Sept.		*D. medioparva* *Scaptomyza* sp.	
Calathea insignis	April thru Oct.	*D. xanthopallescens*		
Aphelandra micans	Aug. 20 to *Dec. 15*	*D. mcclintockae* *flavopilosa* sp. *flavopilosa* sp. *D. busckii*	*D. fasciola* *D. repleta* *D. neomorpha* *D. medioparva* *tripunctata* sp.	*Zygothrica* sp. *Zygothrica* sp.
Calathea allouia	Sept. thru Nov.	*flavopilosa* sp.	*D. medioparva*	*Zygothrica* sp.
Calathea sp.	Sept. thru Nov.			*Zygothrica* sp.
Centropogon coccineus	Sept. thru April	*D. busckii*	*D. medionotata* *D. blumelae* *D. medioparva* *tripunctata* sp. *D. mediocris* *cardini* sp. *Clastopteromyia* sp.	*Zygothrica* sp. *Zygothrica* sp.
Erythrina berteroana	Oct.		*D. medionotata* *D. bodemannae* *D. angustibucca* *D. fasciola* *guarani* sp.	*Zygothrica* sp.
Aroid sp.	Oct.		*D. neomorpha* *D. capricorni* *D. cardinoides* *D. fasciola* *peruviana* sp.	
Myrosms guapilensis	Sept. thru Nov.	Undescribed *Drosophila* sp. (one occasion)		
Heliconia villosa	Sept., Oct.			
Heliconia sp.	Sept., Oct.		*D. mediocris*	
Solanum rubidum	Nov. thru Jan.	*flavopilosa* sp.		

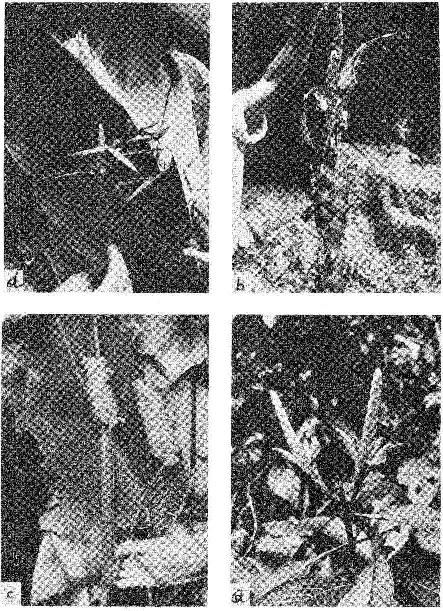

FIG. 2. Photographs of plant hosts of monophagous drosophilids at Cerro Campana, Panamá, 2,500 feet. (a) *Aphelandra micans*; (b) *Calathea insignis*; (c) *Heliconia subulata*; (d) *Heliconia vellerigera*.

Drosophila. *D. xiphiphora* showed less specificity by using the flowers of two *Heliconias*, each also occupied by a monophagous drosophilid; i.e., *Heliconia subulata* and *Heliconia vellerigera*, respectively. Ten species of *Drosophilidae* shared *Aphelandra micans* with *D. mcclintockae* (see Table 1), but the non-host specific flies were bred in far lower numbers than was *D. mcclintockae* from this plant. Of 1,614 flies bred from *Aphelandra micans*, 95.7% were *D. mcclintockae*. Similarly, of 156 flies bred from *Heliconia vellerigera*, 96.2% were *D. hansoni*; 3.7%, *D. xiphiphora*. Of 58 flies bred from *Heliconia subulata*, 94.9% were *D. nigrasplendens*; 4.0%, *D. xiphiphora*; and a single fly belonging to the *flavopilosa* species group was bred from this plant.

Eggs of *D. hansoni*, *D. nigrasplendens*, and *D. mcclintockae* were laid on tough, unopened flower buds scarified by the ovipositor of the female flies. Thus *D. mcclintockae* eggs were found predominantly on the upper half of the flower spike on the outside of the calyx lobes rather than at the base on open flowers. The larvae penetrated the buds and fed on pollen and other plant tissue. In these cases flies could not be bred from fruits or other parts of the respective host plants. By picking away the calyx lobes, *D. mcclintockae* larvae were usually seen feeding around the anthers in immature florets and could be found also in decaying portions of the rhachis. Presence of *D. mcclintockae* larvae in a bud of *Aphelandra micans* could prevent blossoming of the floret involved; but even at the peak of population of the fly, there were more potential florets than flies bred from a flowering spike of the plant. The drosophilid infestation may have caused unopened buds of *Heliconia vellerigera* and of *Heliconia subulata* to drop prematurely. When collected from the ground, the respective host specific *Drosophila* could be bred from these buds. The plants in question suffered little since flowers to spare were produced.

All of the plant species serving host specific drosophilids possessed long flowering periods of from four to nine months, as Table 1 shows. Two of the plants supporting host specific *Drosophila*, i.e., *Heliconia subulata* and *Heliconia vellerigera*, with long flowering periods, began to blossom in the dry season and so supported their respective *Drosophila* species during a time of the year when certain ground-feeding drosophilids existed in very low numbers (Pipkin, 1965a).

The fluctuation in population size of a host specific drosophilid was correlated with the time of blossoming of its respective plant host. Each of the plant species supporting such *Drosophila* at Cerro Campana, i.e., *Calathea insignis*, *Heliconia vellerigera*, *Heliconia subulata*, and *Aphelandra micans*, began to blossom for one or two months before adult flies of the respective species could be collected. This indicates that another plant host was not being used. Fluctuations in population size of *D. mcclintockae* have been followed in most detail. The egg of this fly could be distinguished from that of all other species of *Drosophila* collected at Cerro Campana. Since the species could be cultured in the laboratory, it was possible to determine that eggs of *D. mcclintockae* are unusually long and possess three filaments each more than twice the length of the egg (Pipkin, 1964). *D. trifiloides*, also occurring at Cerro Campana, has smaller eggs with three short egg filaments, yellow at the base. Other *Drosophila* species there have two, four, or no egg filaments. For this reason the association of *D. mcclintockae* with its host plant, *Aphelandra micans*, could be traced by observing eggs both before and after adult flies could be collected. Thus, on August 21, 1962, when *Aphelandra micans* was just beginning to flower, eight eggs of *D. mcclintockae* were found on two of 27 floral spikes examined. On September 19, one inflorescence bearing four eggs of *D. mcclintockae* was observed whereas 29 inflorescences carried no eggs, but five *D. mcclintockae* were bred out. On October 3, although no egg counts were made, still no adult *D. mcclintockae* were seen. A month later, on November 2, one or more of these large drosophilids was crawling on nearly every plant. Seven adults were counted on five spikes of the same plant in ten minutes. The numbers of *D. mcclintockae* adults bred out increased from 2.3 per floral spike collected October 3 to 10.4 flies per spike collected November 2, and dropped to 5.5 flies per spike collected November 13. Twelve, 33, and 35 floral spikes, respectively, were tested singly in half-pint jars for the three collections. It is estimated from counts, that 300 inflorescences of *Aphelandra micans* were present in the collecting area at the height of the flowering period of this plant. The plant was uncommon in other parts of Cerro Campana which were visited in the four years of collecting. Thus, the peak population size of *D. mcclintockae* in the collecting area was of the order of 3,400 individuals.

Aphelandra micans was no longer blossoming after mid-December. The fruiting spikes turned from bright red to brownish green, but some red color was left in the lower bracts. On January 15, 1963, many fruiting spikes of *Aphelandra micans* were seen. Those in the open area around the coffee finca were drying out and dropping off. At this time 77 eggs of *D. mcclintockae* were observed on 11 of 13 fruiting spikes, but only one adult female fly was bred from these. On February 7, 157 eggs of *D. mcclintockae* were counted on 15 of 23 fruiting spikes of *Aphelandra* plants growing in deep forest. Subsequently, no traces of larvae or pupae were seen in these spikes and no adult flies were bred from them. Seven fruiting spikes of *Aphelandra micans* collected from forest on March 15, 1963 bore no eggs of *D. mcclintockae*, but three of four spikes collected on March 28, 1963 carried 11, 2, and 1 eggs, respectively. No adults were bred from these. No other fruiting spikes of *Aphelandra micans* were seen at this time. On April 18, the last two fruiting spikes of *Aphelandra micans* were located in deep forest. No eggs of *D. mcclintockae* were seen on them and no flies bred from them. During the four years of collecting in the forest at Cerro Campana, flowers of plants other than *Aphelandra micans*, listed in Table 1, were examined repeatedly without success for the presence of *D. mcclintockae* eggs. A catastrophic reduction in population numbers of *D. mcclintockae* must occur yearly at the end of the flowering period of

Aphelandra micans. This is shown by the large numbers of eggs laid in early January on fruiting stalks of the plant which yielded no further generations of *D. mcclintockae.* It must be concluded that a few adults of *D. mcclintockae* undergo diapause and survive the period when *Aphelandra micans* is not blossoming, from January to some time in August. This is borne out by the long period after *Aphelandra micans* began to flower each year before the population of the fly reached sufficient numbers for imagines to be collected.

No *D. mcclintockae* imagines were bred from two other forest growing species of *Aphelandra*; i.e., *Aphelandra sinclairiana* from Madden Forest, Canal Zone, on April 4, 1963 (33 floral spikes tested) and *Aphelandra tetragona*, from forest in Uroseka (near El Real, Panamá) on November 24, 1962 (25 floral spikes tested). On the other hand, *D. mcclintockae* was bred from an undescribed *Aphelandra* species, very close to *Aphelandra micans*, collected at Yape, near El Real, Panamá, on November 23, 1962. The plant possessed yellow flowers and bright orange-red bracts in contrast with the red flowers and red bracts of *Aphelandra micans*. The inflorescence of the undescribed species was about 14 inches, longer than is usual in *Aphelandra micans.* In Almirante, Panamá, *D. mcclintockae* was bred from *Aphelandra micans.* The longer wet season at Almirante on the Caribbean side of the isthmus accounts for the blossoming of the host plant in April when the fly was collected.

There was no evidence of competition for larval food supply between the monophagous *D. mcclintockae* and 10 polyphagous species of *Drosophila* (see Table 1) undergoing synchronous development with *D. mcclintockae* in flowers of *Aphelandra micans.* Little fluctuation in numbers of the polyphagous species bred from *Aphelandra micans* accompanied the autumn population expansion of *D. mcclintockae* bred from this plant. The number of individuals of polyphagous *Drosophila* bred per inflorescence varied from 0.5 from the collection of September 19, 1962 (compared with 0.17 of *D. mcclintockae*), to 0.75, October 3 (compared with 2.3 individuals of *D. mcclintockae*); 0.61, November 2 (compared with 10.4 individuals of *D. mcclintockae*); 0.12, November 13 (compared with 5.5 individuals of *D. mcclintockae*). In 1961, the number of individuals of polyphagous *Drosophila* bred per inflorescence was 0.10 from the October 4 and October 11 collections (compared with 1.4 *D. mcclintockae* per inflorescence); 0.16 from the October 25 and October 28 collections when 1.6 individuals of *D. mcclintockae* were bred out, and 0.50 on November 12 when *D. mcclintockae* reached 2.9 individuals bred per inflorescence. On November 16, 1963, when the *D. mcclintockae* population was expanded to 16.7 individuals per inflorescence of *Aphelandra*, still 0.15 individuals of polyphagous species of *Drosophila* were bred out. These data support the conclusion that larval food supply and "living space" for larval development afforded by *Aphelandra micans* is more than sufficient for both polyphagous and the monophagous flies using this plant.

Plants supporting monophagous *Drosophila* species in areas other than Cerro Campana, Panamá, are listed in Table 2 with their respective drosophilids. In separate additional columns of Table 2 appear non-host specific *Drosophila* also bred from the plants and all *Drosophila* aspirated or netted from them.

The results of 26 field collections made in the forest of the Fort Sherman Reservation, Canal Zone, on the Caribbean side of the isthmus, showed three apparently monophagous *Drosophila* species (see Table 2). *D. alexanderae* is restricted to *Heliconia elongata*. Similarly, *D. alani* was bred only from flowers of *Heliconia curtispatha*, and *D. leukorrhyna* was bred only from flowers of *Heliconia mariae*. Flowers of the latter host plant from Madden Forest, Canal Zone, likewise yielded only *D. leukorrhyna*. However, both *D. leukorrhyna* and *D. alani* (or a subspecies or a closely related species of *D. alani*) were netted from *Heliconia mariae* in El Real, Panamá, and both species (or subspecies or closely related species) were bred from a third host, *Heliconia rostrata* in Rio Raposo, Colombia. The three *Heliconia* hosts, *H. mariae*, *H. curtispatha*, and *H. rostrata*, are relatively closely related within the genus, displaying several important charac-

TABLE 2

Plants supporting host specific *Drosophila* from areas other than Cerro Campana, Panama

Plant	Area	Host specific flower-feeder bred out	Non-host specific flower-feeder bred out	Flies aspirated or netted
Heliconia elongata	Almirante, Panama	*D. alexanderae*	*flavopilosa* sp.	
	Ft. Sherman Res., Canal Zone	*D. alexanderae*		
	El Real, Panama	*D. alexanderae*		
	Trinidad, W. I.			*D. alexanderae*
Heliconia curtispatha	Almirante, Panama	*D. alani*		
	Ft. Sherman Res., Canal Zone	sp. near *D. alani*	*flavopilosa* sp. *D. busckii*	sp. near *D. alani* *D. othoni*
	El Real, Panama	sp. near *D. alani*		
Heliconia mariae	Ft. Sherman Res., Canal Zone	*D. leukorrhyna*		*D. leukorrhyna* *D. othoni*
	Madden Forest, Canal Zone	*D. leukorrhyna*	*flavopilosa* sp.	
	Yape near El Real, Panama	*D. leukorrhyna*		sp. near *D. alani*, *D. leukorrhyna*
Heliconia rostrata	Rio Raposo, Colombia	sp. near *D. leukorrhyna* sp. near *D. alani*		
Heliconia collinsiana	Rio Raposo, Colombia			*D. hansonioides*
Calathea lutea	Ft. Sherman Res., Canal Zone	*D. aureopallescens*	*D. busckii*	
	Almirante, Panama	*D. aureopallescens*		
	El Real, Panama	*D. aureopallescens*	*D. othoni*	
	Rio Raposo, Colombia	*D. aureopallescens* *D. xanthopallescens*		
Calathea insignis	El Volcán, Panama	*D. aureopallescens*		
	Rio Raposo, Colombia	*D. xanthopallescens*		

ters in common, such as large size, large, pendulous inflorescence, distichous short crowded bracts of deep red color.

The closely related *D. xanthopallescens* and *D. aureopallescens* show a relative degree of host specificity. *D. aureopallescens* prefers *Calathea lutea* from which it was bred regularly in collections from the Fort Sherman Reservation, but this fly was described from specimens hatching from what is now known to have been *Calathea insignis*, collected in El Volcán, Panamá. *Calathea insignis* is the characteristic host plant for *D. xanthopallescens* at Cerro Campana, where *D. aureopallescens* was never found. However, both these species were bred from the same specimen of *Calathea lutea* collected in Rio Raposo, Colombia.

Table 2 shows that the same or very closely related *Drosophila* species could be bred from the same plant host collected from several different geographical areas. *D. alexanderae* was bred from *Heliconia elongata* collected at Almirante, Fort Sherman Reservation, El Real, and aspirated from this plant at Trinidad. The male and female genitalia, and spermatheceae of *D. alexanderae* from all these areas are indistinguishable, but the body color of the Almirante specimens is darker than that of specimens from areas to the east. *D. leukorrhyna*, bred from *Heliconia mariae* appeared the same if collected in the Canal Zone or in Yape, Panamá (near El Real). The *D. leukorrhyna* specimens from Rio Raposo, Colombia, bred from *Heliconia rostrata*, possessed a yellowish rather than the characteristic whitish carina. Slides of male genitalia of *D. leukorrhyna* from central and eastern Panamá and Rio Raposo, Colombia, showed no differences. It is not known whether the difference in carina color represents a specific or subspecific difference. Three pairs of closely related but distinct species (according to breeding tests) of the *tripunctata* species group differ similarly in carina color but not in male genitalia. These include *D. roehrae* and *D. unipunctata*; *D. metzii* and *D. pellewae*; and *D. medioparva*, and an undescribed sibling species (Pipkin and Heed, 1964). A difference in body color but not in male genitalia was found in specimens of *D. alani* from Almirante in contrast with those of the Canal Zone and El Real, Panamá. The Almirante specimens have lead colored pleura and greenish abdomens. The eastern specimens have tan pleura and brownish abdomens. Thus, in the case of *D. alexanderae*, *D. alani*, and *D. hansoni*, to be considered shortly, the western specimens are more darkly pigmented than the eastern specimens.

Specific differences involving both body color and genitalia distinguish *D. hansoni* of Cerro Campana and a closely related species, *D. hansonioides* (Pipkin, 1965b), of Rio Raposo, Colombia. The two species likewise differ in host plants. *D. hansoni* uses *Heliconia vellerigera*; the closely related drosophilid, *Heliconia collinsiana*. These plants are only fairly closely related within the genus. Both possess pendant inflorescences, but whereas *Heliconia vellerigera* has a hairy inflorescence with wavy rhachis, *Heliconia collinsiana* has a smooth inflorescence with more sinuous rhachis. Both topographic as well as habitat isolation could be responsible for the differentiation of these closely related *Drosophila* species.

Drosophila nigrasplendens, regularly bred from *Heliconia subulata* (Fig. 2a) at Cerro Campana, Panamá, was either bred or collected from three other closely related *Heliconia* species (Fig. 3e, f, h) over a wide range of distribution: Trinidad, W. I.; Fort Sherman Reservation, Canal Zone, on the Caribbean side of the isthmus; and Leticia, Colombia. The male genitalia of *D. nigrasplendens* specimens from these areas are indistinguishable. *D. xiphiphora* which shares *Heliconia subulata* (Fig. 2a) with *D. nigra-*

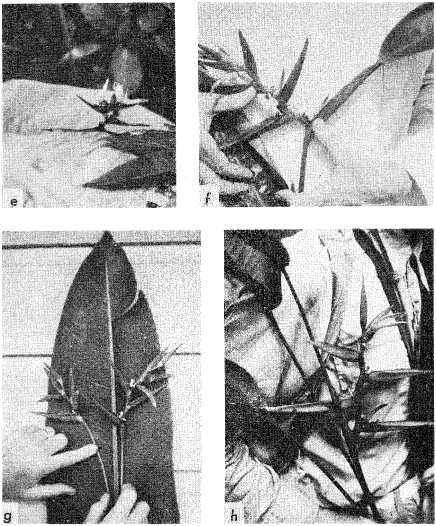

FIG. 3. Photographs of closely related *Heliconia* species from different geographical areas supporting either *D. nigrasplendens*, *D. xiphiphora*, or both. (e) *Heliconia psittacorum* (Trinidad, W. I.); (f) *Heliconia* sp. A (Fort Sherman Reservation, C. Z.); (g) *Heliconia* sp. B (El Real, Panamá); (h) *Heliconia schneeana* (Leticia, Colombia).

splendens at Cerro Campana, was bred from closely related *Heliconia* species at El Real, Panamá (Fig. 3g), and Leticia, Colombia (Fig. 3h). In Trinidad, W. I., the host plant of *D. nigrasplendens* is *Heliconia psittacorum*. Table 4 indicates the host plants for these two drosophilids in different geographical areas. The five closely related Heliconias are similar in the structure of the inflorescence, as may be seen from Fig. 2a and Fig. 3e–h, but they differ in plant height and flower color. *Heliconia subulata* (Fig. 2a) has green bracts, pink flowers, and varies from 3 to 20 feet in height. *Heliconia psittacorum* (Fig. 3e) has orange and red tipped bracts, orange flowers, and is from 3 to 5 feet in height. Bracts of species A (Fig. 3f), from Fort Sherman Reservation are red; flowers, yellow tipped with green; and the plants about 20 feet high. *Heliconia* B, from El Real (Fig. 3g) has green bracts; flowers red tipped with buff; and grows about 6 feet high. Finally, *Heliconia schneeana* (Fig. 3h) from Leticia, Colombia, has red bracts, green flowers, and varies from 6 to 8 feet in height.

2. *Polyphagous flower-feeding Drosophila*

Polyphagous flower-feeders use flowers of several plant species in one geographical area. At Cerro Campana these included *D. busckii* and two members of the *flavopilosa* species group. Twelve species of ground-feeders and several fungus-feeders were also bred from flowers serving polyphagous flower-feeders in this area as Table 1 shows. With the exception of *Centropogon coccineus*, these plants exhibited short flowering periods of from one to three months.

Table 3 lists plants supporting non-host specific *Drosophilidae* from regions other than Cerro Campana. Flower-feeding, ground-feeding, and fungus-feeding species appear in separate columns of the table. The cosmopolitan species, *D. busckii* was bred from flowers broken off plants of seven different species. Four of these also supported monophagous *Drosophila* (see Table 3). *D. busckii* was also bred from fruit of an unidentified forest tree near El Real, Panamá, but it never entered traps baited with cultivated fruits in the forest collecting stations of Panamá. In The Lebanon, Pipkin (1952), found *D. busckii* in small numbers in such traps. The cosmopolitan *D. immigrans* was bred from flowers of the introduced plant *Hedychium coronarium* from a house yard in El Volcán, Panamá, collected by net sweeping over fallen blossoms in São Paulo, Brasil, by Professor C. Pavan, and trapped with fruit bait by Professor O. Frota-Pessoa on the islands of Angra dos Reis. The drosophilid thus shows a wide adaptability in its food habits which is reflected in its wide range.

Seven as yet unidentified members of the *flavopilosa* species group were collected and bred from 14 different plant species (see Table 3). Many of these plants belong to different families and most support several polyphagous drosophilids. In two collecting areas, two members of the *flavopilosa* species group were bred from flowers of *Hedychium coronarium*. In both instances these were bred from the same floral specimen on the same day. Wheeler, Takada, and Brncic (1962) found *D. flavopilosa* breeding in the

TABLE 3

Plants supporting non-host specific *Drosophilidae* from areas other than major collecting station at Cerro Campana, Panama (2500 ft.)

Plant	Area	Flower-feeder bred out	Ground-feeder bred out	Fungus-feeder bred out
Woody vine (legume)	Camaron, Panama	*D. sticta* *flavopilosa* sp. *flavopilosa* sp.	*D. crocina* *D. mediostriata* *D. albirostris*	
Heliconia latispatha	Base of Cerro Campana, Panama	*flavopilosa* sp.	*D. fasciola* *D. cardinoides*	
Helianthus sp.	Base of Cerro Campana, Panama		*D. medionotata* *Clastopteromyia* sp.	
Hedychium coronarium	El Volcán, Panama	*D. sticta* *flavopilosa* sp. *D. immigrans* *D. busckii*	*D. melanogaster*	*Zygothrica* sp.
	Panama City, Panama	*flavopilosa* sp.	*D. cardinoides*	
	Cerro Campana, Panama 2200 ft.	*D. sticta* *flavopilosa* sp. *flavopilosa* sp.	*D. melanogaster* *D. ananassae* *D. cardini*	*Zygothrica* sp.
	El Real, Panama	*flavopilosa* sp.	*D. ananassae*	*Zygothrica* sp.
	Rio Raposo, Colombia	*flavopilosa* sp. *D. sticta*	*D. crocina*	
Dimerocostus uniflorus	Almirante, Panama	*flavopilosa* sp.		*Zygothrica* sp. *Zygothrica* sp.
	Ft. Sherman Res., Canal Zone	*D. leoni* *flavopilosa* sp.	*C. opaca*	*Zygothrica* sp. *Zygothrica* sp.
	El Real, Panama	*D. leoni*		*Zygothrica* sp.
	Rio Raposo, Colombia	*D. tibialis*		
Costus splendens	Almirante, Panama	*D. leoni* *flavopilosa* sp.		*Zygothrica* sp.
Costus villosissimus	Ft. Sherman Res., Canal Zone	*D. tibialis* *flavopilosa* sp.	*D. medionotata*	
	Summit Gardens, Canal Zone	*D. tibialis*	*D. albirostris*	*Zygothrica* sp. *Zygothrica* sp.
Ochroma limonensis	Sona, Panama	*flavopilosa* sp.		
Musa sapientum	Almirante, Panama	*flavopilosa* sp.		
Malvaviscus arboreus	Cerro Punta, Panama	*flavopilosa* sp.		
Carludovica palmata	Madden Forest, Canal Zone		*D. nebulosa* *willistoni* sibling species	
Datura arborea	El Volcán, Panama	*D. busckii*	*repleta* sp.	
Unknown vine blossom	El Volcán, Panama	*D. busckii*		
Domestic lily	El Real, Panama	*flavopilosa* sp.	*D. ananassae*	*Zygothrica* sp.
Calathea violaceae	Base of Cerro Campana, Panama	*flavopilosa* sp. *flavopilosa* sp.	*D. cardinoides*	*Zygothrica* sp.
	El Real, Panama		*D. ananassae*	*Zygothrica* sp.

solanaceous plant *Cestrum parqui* in Chile. At Cerro Campana, one member of this group was bred from *Solanum rubidum* and also from *Aphelandra micans*, but *flavopilosa* group species were not bred from several plants supporting ground-feeding *Drosophila* at Cerro Campana. Like *D. busckii*

TABLE 4

Flower-feeding *Drosophila* bred or collected from *Heliconia subulata*, *Heliconia psittacorum*, and three other closely related species.

Plant host	*Drosophila* species	Locality
Heliconia subulata	*D. nigrasplendens* *D. xiphiphora* (bred)	Cerro Campana, Panama
Heliconia sp. A	*D. nigrasplendens* (bred)	Ft. Sherman Reservation, Canal Zone
Heliconia Sp. B	*D. xiphiphora* *flavopilosa* sp. *flavopilosa* sp. (bred)	El Real, Panama
Heliconia schneeana	*D. nigrasplendens* *D. xiphiphora* (bred)	Leticia, Colombia
Heliconia psittacorum	*D. nigrasplendens* (aspirated)	Trinidad, W. I.

and *D. ~~flexipilosa~~*, the polyphagous flower-feeders of the *flavopilosa* species group have a wide distribution.

Two distantly related *Drosophila* species, *D. tibialis* and *D. leoni*, were found to share flowers of *Dimerocostus uniflorus* and of several species of *Costus* in collections from western Panamá to Rio Raposo, Colombia. A degree of host specificity is indicated when an aggregation of *Drosophila* species uses several related plant species.

3. *Adaptations in flower-feeding Drosophila to plant hosts*

Structural adaptations in ovipositor, egg filaments, and color of imagines may indicate certain characteristics of the flowers of the plant host used. The tip of the ovipositor is acuminate in females of monophagous drosophilids ovipositing on tough fleshy flower buds, (e.g., *D. nigrasplendens*, *D. alani*, *D. alexanderae*, *D. mcclintockae*, and *D. hansoni*, Fig. 4j–n). The tip of the ovipositor is rounded in *D. xanthopallescens*, *D. aureopallescens*, *D. flexipilosa*, and *D. leoni* which deposit eggs on soft open flowers or in juices held by calyx buds (Fig. 5o–r). The shape of the ovipositor does not always indicate whether soft or tough floral tissue is being used because ovipositors of members of the *flavopilosa* species group are uniformly acuminate. These flies deposit eggs on relatively tough as well as in soft flowers. For rasping floral tissue, the ovipositors of *D. alani*, *D. alexanderae*, *D. mcclintockae*, and *D. hansoni* possess medial as well as peripheral spines (Fig. 4k–n). The extreme elongation of the ovipositor in *D. xiphiphora* is an adaptation for placing a single egg within a small bud less than two inches long (Fig. 6t). Absent or rudimentary filaments were observed in eggs of *D. xiphiphora* (Fig. 6s), *D. leoni* (Fig. 7u, w) and *D. nigrasplendens* (Fig. 7x). Since the egg of the first species is inserted inside an unopened flower bud, no filament is needed. Newly laid eggs of *D. leoni* contain actively moving larvae which soon emerge. Egg filaments

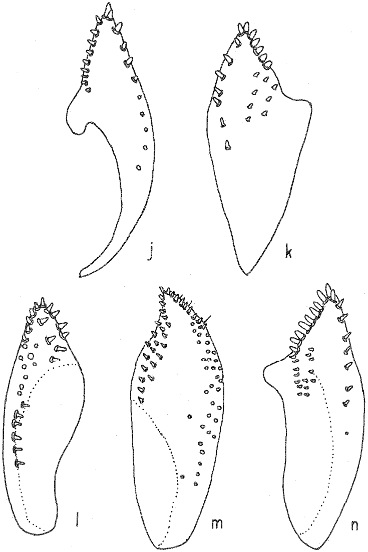

FIG. 4. Ovipositors of *Drosophila* laying eggs on tough unopened buds. (j) *D. nigrasplendens*; (k) *D. alani*; (l) *D. alexanderae*; (m) *D. mcclintockae*; (n) *D. hansoni*.

are not needed in a viviparous form. The long egg filaments of *D. mcclintockae* and the oar-shaped filaments of *D. hansoni* (Fig. 7v) provide a mechanism for attachment of the egg to the floral hairs of the respective plant hosts.

Imagines of *D. mcclintockae* are adaptively colored to the extent that the collector's eyes often were deceived when the flies were resting on inflorescences of *Aphelandra micans*. The fly's eye color matches the red of the flower. The dark wings of the fly resemble a darkened decaying calyx lobe subtending a fully opened flower. On several occasions a small fly-

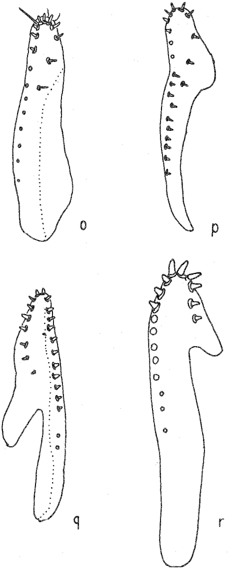

FIG. 5. Ovipositors of *Drosophila* laying eggs on soft open flowers or in juices held by calyx lobes. (o) *D. xanthopallescens*; (p) *D. aureopallescens*; (q) *D. flexipilosa*; (r) *D. leoni*.

catcher was observed feeding in a thicket of *Aphelandra micans* during a time of peak of population of *D. mcclintockae*, presumably catching the flies. Thus, the color pattern of the imagines may have been adaptive in deceiving the birds. The pale yellow color of *D. xanthopallescens* and the orange color of *D. aureopallescens* blend with the greenish yellow calyx lobes of *Calathea insignis* and the bronze calyx lobes of *Calathea lutea*, respectively.

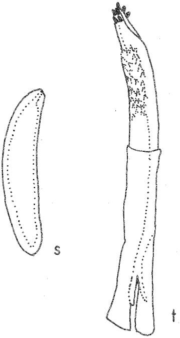

FIG. 6. Egg (s) and ovipositor (t) of *D. xiphiphora*.

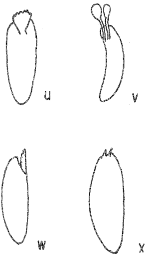

FIG. 7. Egg of *D. leoni* (u and w); *D. nigrasplendens* (x); and *D. hansoni* (v).

4. *Cultivation of flower-feeding drosophilids in the laboratory*

Seven members of the polyphagous *flavopilosa* species group and *D. sticta* are being successfully cultured on laboratory medium. Efforts to culture *D. leoni* and *D. othoni* failed. A few specimens of *D. tibialis* were reared one generation on laboratory medium. The medium used contained 8 quarts of water, 3 cups corn meal, 1½ cups dried Standard Brands yeast number 2019, 8 ounces of karo syrup, 2 tablespoons powdered agar; 12 cc furfural (10% solution in 95% alcohol). This soft, moist medium was inoculated with live yeast of the *y*-2 strain originally isolated from cactus by Wagner (1949). This yeast apparently competes with mold growth, thus necessitating only a minimum of mold inhibitor which is toxic also to the delicate tropical species.

Among host specific *Drosophila* species, *D. alani*, *D. leukorrhyna*, *D. alexanderae*, and *D. xanthopallescens* were never bred in large numbers at one time from their respective host plants and none could be cultured on the laboratory medium. Gravid females of *D. hansoni* collected in nature would deposit eggs on laboratory medium, but no development occurred. *D. aureopallescens* could be bred in large numbers from *Calathea lutea*. When these drosophilids were held in crowded conditions and transferred to fresh, wet medium every other day, the females began to lay eggs after about 10 days. Larval development was slow, but proceeded to pupation when most of the flies died. Only three imagines ever emerged from numerous pupae obtained on different occasions and these did not produce another generation.

It has been possible to culture successfully for two years the monophagous *D. mcclintockae*. Flies were bred in large numbers from the host plant, held under crowded conditions for a week. At the end of this time eggs were laid, and when larvae were actively moving about, the crowded contents of three vials were transferred to a half-pint milk bottle with culture medium. Later the fly could be cultured entirely in half-pint milk bottles. It has now become adapted to the extent that oviposition does not seem to be excessively delayed. Nevertheless, bottles must be crowded with females for oviposition to occur and not all pupae eclose.

DISCUSSION

Among *Drosophila* species both feeding and breeding in living (not fallen) flowers of neotropical forest, varying degrees of plant host specificity are found. Ecological isolation in a single area is not complete for *D. xanthopallescens* and its sibling species, *D. aureopallescens*. The first species prefers *Calathea insignis*; the second, *Calathea lutea*; but each has been bred from both species of *Calathea*. Isolation of closely related species of *Drosophila* is further advanced in the case of *D. leukorrhyna* and *D. alani*, belonging to the same species group (Pipkin, 1964). In various parts of Panamá, *D. leukorrhyna* has been bred consistently from *Heliconia mariae*; and *D. alani*, from *Heliconia curtispatha*. However, both species of *Drosophila* were netted at the same time from *Heliconia mariae* in eastern Panamá. Kinsey (1936) likewise found closely related species of gall wasps (*Cynipidae*) on distinct but related hosts. Habitat isolation in a given locality is complete for drosophilids with a single plant host such as *D. nigrasplendens*, *D. hansoni*, and *D. mcclintockae* at Cerro Campana, Panamá.

The same plant host may be used by a monophagous drosophilid (or its subspecies or closely related species) from widely separated geographical areas. For example, *D. alexanderae* from western Panamá uses *Heliconia elongata*. Its lighter subspecies (or closely related species) depends on the same host plant from central Panama to Trinidad, W. I. On the other hand, changes in plant hosts may occur where there is a history of long geographic isolation. Thus, *D. hansoni* at Cerro Campana, uses *Heliconia vellerigera*; but the closely related species, *D. hansonioides*, depends on *Heliconia collinsiana* in Rio Raposo, Colombia. South America was separated by an oceanic barrier from parts of Central America during most of the Tertiary. *Heliconia vellerigera* and *Heliconia collinsiana* are fairly closely related. Similarly, *D. leukorrhyna* and *D. alani* in Panamá have been bred only from *Heliconia mariae* and *Heliconia curtispatha*, respectively, but both species (or subspecies or closely related species) have been bred from *Heliconia rostrata* at Rio Raposo, Colombia. Geographical isolation has led to slight body color differences in strains of each of these *Drosophila* species and also to an evolution in the direction of monophagy in Panamá. This sort of evolution was predicted by Dethier (1954).

A recent change in host plant preference appears to have taken place for members of the polyphagous *flavopilosa* species group. Females of these species have acuminate tipped ovipositors armed with prominent peripheral spines similar to those found on monophagous drosophilids ovipositing on tough, unopened flower buds. *Flavopilosa* group species develop both in tough flower buds of various plant species as well as in plant species with soft buds and large open flowers, among them, *Hedychium coronarium*, an introduced plant.

In the case of the widely distributed *D. nigrasplendens*, the species splitting of the host plant appears to have progressed more rapidly than that of the drosophilid. In different geographical areas the fly uses flowers of the closely related *Heliconia subulata*, *Heliconia psittacorum*, *Heliconia schneeana*, and an undescribed species as hosts. Morphologically *D. nigrasplendens* is similar in the different areas, but it is not possible to make breeding tests to ascertain the extent of cryptic genetic divergence. The host plants are structurally quite similar, but there are differences in the color of flowers, bracts, and fruits. The association of the distantly related *D. xiphiphora* and *D. nigrasplendens* in three of these *Heliconia* species strengthens the suggestion that the host dependence of the two *Drosophila* species antedates the species splitting of the ancestral *Heliconia*. Fossil *Heliconia* have been reported from the Middle Miocene of Venezuela, Cuba, and Trinidad (Berry, 1921, 1939, 1925) and the Pliocene of Colombia and Bolovia (Berry, 1922). This author states that tertiary plant genera of Acre, Brasil, recognized as fossils of late Pliocene (Berry, 1937) and those of the same date of Colombia (Berry, 1945) are all represented in present flora of these regions by closely related similar species. Since the ancestor of *Heliconia psittacorum* has differentiated into five closely related species, it is possible to believe that the association of *D. nigrasplendens* and *D. xiphiphora* dates back to the Pliocene at least.

Host preference of monophagous leaf-eating insects depends chiefly on attractant and repellant compounds in the leaves rather than on compounds necessary as food substances for normal larval development according to Dethier (1954), Fraenkel (1953), and Painter (1953). The preference of *D. mcclintockae* for *Aphelandra micans* fits this hypothesis. This fly oviposits both on the flowering and on the fruiting spike of the host plant in spite of the fact that larval development is possible only on the flowering spikes (the larvae are pollen feeders). When oviposition of *D. mcclintockae* is artificially induced by holding the females under crowded conditions, development is sufficiently normal for cultures of the fly species to be maintained. *D. aureopallescens* can be forced by crowding to oviposit on laboratory medium. The prolonged larval period and failure to eclose may depend upon differences in relative humidity between laboratory bottle and the semi-liquid contents of the calyx pockets of the host plant.

The occurrence of monophagous flower-feeding *Drosophila* species in the neotropical forest where highly successful multispecific aggregations of polyphagous species of *Drosophila* exist is due to the advantage of exploiting an additional niche. Although a single-host drosophilid comprises about 95% of the insect output of its host plant, still as great a variety of polyphagous species of *Drosophila* (eight species) also may be bred during the wet season from such a plant as from another plant in the same plot supporting only polyphagous drosophilids. A limit of three to four monophagous species of *Drosophila* per locality appears to depend upon the presence in each locality of only three or four plant species with long flowering periods and occurring in sufficient numbers to support a *Drosophila* population.

In discussing the ecological regulation of species diversity, Connell and Orias (1964) argue that owing to a great stability of the physical environment in the tropics, "less energy is required for regulatory activities; that is, those that counter the challenges offered by the environment." Thus more energy remains for growth and reproduction resulting in large populations which are rather sedentary and become semi-isolated in the favorable environment. With the formation of species interrelationships, new niches are formed, promoting the splitting of species, according to these authors. Connell and Orias (1964) question the conclusion of Fischer (1960) that the increased diversity of species in the tropics over what is found in temperate areas depends simply on the longer period of undisturbed evolution in the tropics. On the other hand, the greater stability of modern neotropical environment compared with that in temperate areas is certainly only relative. Much of present-day neotropical forest, although enjoying a rather constant temperature throughout the year, possesses a distinct wet and dry season (Bennett, 1963) with pronounced effects on the seasonal fluctuations of various aggregations of *Drosophila* species (Pipkin, 1965a; Pipkin, 1953). In Panamá, only two ground-feeders, *D. emarginata* and *D.*

fulvimacula, were present in fairly constant numbers throughout the year. Other species showed pronounced fluctuations either in the wet or in the dry season, depending on their food habits. According to Connell and Orias, (1964), the productive stable communities are supposed to produce larger populations which later become differentiated into a larger number of species. Nowadays the ground-feeding *Drosophila* in Panamá with the largest populations are the fleshy fruit breeders, but the number of species in this aggregation is only about 3/4 the number in the aggregation which breeds in small drier fallen fruits and blossoms (Pipkin, 1965 a).

The present study on neotropical flower-feeding *Drosophila* bears out the emphasis Connell and Orias (1964) have placed upon the promotion of niche diversity by interspecies relationships. Many examples of such relationships exist between species of *Drosophila* in the neotropical forest. For example, immature developmental stages of flower-feeders are passed entirely in living flowers which only augment the sites in which larval and pupal development of fungus and ground-feeders takes place. Only small numbers of individuals of polyphagous flower-feeders use the host plant of a monophagous drosophilid. Distantly related *Drosophila* species such as *D. tibialis* and *D. leoni* (or *D. nigrasplendens* and *D. xiphiphora*) consistently share a host plant species over a wide geographic area.

SUMMARY

A study has been made of plant host specificity of flower-feeding *Drosophila* collected in western, central, and eastern Panamá, the west coast of Colombia, Trinidad, W. I., and Leticia, Colombia, on the headwaters of the Amazon River. Three and four species of single host flower-feeding *Drosophila* species were found in each of two collecting areas, respectively, in central Panama. These flies were bred only from flowers of their special hosts and never from other plants in the vicinity. A fluctuation of population numbers of the drosophilid is correlated with the period of blossoming of the plant species. Monophagous flower-feeding *Drosophila* occupy plants with long blossoming periods of four to nine months. Other adaptations of monophagous drosophilids to the host plant concern body color and structural details of the ovipositor and egg filaments. About 5% of flies bred from flowers of plants serving monophagous *Drosophila* are polyphagous drosophilids; i.e., flower-feeders, ground-feeders, or fungus feeders. No evidence was found of larval competition between a monophagous *Drosophila* species and a polyphagous drosophilid sharing the same plant. Polyphagous flower-feeding drosophilids use a variety of host plants which generally have a short blossoming period of one to three months. These more versatile species have a wide range of distribution and include the cosmopolitan *Drosophila busckii.* Preferences for one plant host but tolerance for another have been found in the case of two sibling species of *Drosophila* using, respectively, two different members of the genus *Calathea* as primary hosts and each having as secondary host the primary host of its sibling *Drosophila* species. In addition, two monophagous flower-feeders

belonging to the same species group use two different *Heliconia* species in the same area. In different geographical areas, a monophagous *Drosophila* species depends either on the same plant host or on plant species very closely related within the genus. An association of the same two distantly related host specific drosophilids in different geographical areas is presumed to have been established in the Pliocene at least, antedating the differentiation of the ancestral *Heliconia* into five closely related plant species.

A number of polyphagous flower-feeding *Drosophila* species can be cultured on laboratory medium. With one exception monophagous flower-feeders on this medium either (1) refuse to oviposit, or (2) undergo a prolonged larval and pupal state and fail to eclose. It has been possible to adapt one host specific *Drosophila* species to laboratory culture medium.

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