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ABSTRACT: The influence of feeding and breeding habits upon population size was investigated in 73 species of neotropical forest-dwelling Drosophilidae. Three classes of ground feeders are defined according to fruit preferences and attractability to traps baited with cultivated fruits. Class A species prefer small drier fallen fruits and blossoms both for adult feeding and larval breeding and enter traps to a limited degree. Class B species use fleshy fruits in addition to these, and enter traps to a moderate extent. Class C species use chiefly fleshy fruits for breeding, and show a strong inclination to enter traps. As a consequence of their feeding and breeding habits, class A species undergo population expansions, where such occur, in the wet season when their fruits and blossoms suffer less from desiccation. Class B and some class C species undergo expansions in the dry season since they are able to use fleshy fruits. Some class C species exhibit nonseasonal fluctuations. The range of mean sizes of minimal population samples of class A and B species collected by net sweeping is similar to that of class C species collected by trapping. Because they utilize fleshy fruits for breeding, most class B and C species are collected in expanded populations far oftener than class A species. Larval development of different species of ground-feeding *Drosophila*, including members of the same species group or even of the same sibling set, generally occurs almost synchronously, although successional development has been observed. Since the number of species netted from a given fruit greatly exceeds the number of species bred from a limited volume of the fruit, a type of interference between species during oviposition has been inferred.

INTRODUCTION

Natural feeding and breeding sites are known for relatively few species of *Drosophila* because most collections have been made by trapping with cultivated fruits as bait. Wagner (1944, 1949) studied members of the repleta species group breeding in *Opuntia lindheimeri*. Carson and Stalker (1951) found *D. robusta* breeding in sap exudations of elms and 12 other species of deciduous trees. Carson (1951) located the breeding sites of *D. pseudoobscura* and *D. persimilis* in slime fluxes of the California black oak, *Quercus kelloggi*. Yeasts isolated from the crops of adults flies of these species differed from

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yeasts isolated from the breeding sites, showing that the flies do not oviposit and feed in the same locations.

Adults of 14 *Drosophila* species at Mather, California, exhibited food preferences among different species of yeasts isolated from the crops of individuals taken in nature (Dobzhansky *et al.*, 1956). The same was true for certain Brazilian species collected by trapping (Da Cunha *et al.*, 1957). These authors concluded that the *Drosophila* studied were able to feed on several different yeasts, but that each species had preferences that varied in degree of choice. Lindsay (1958) and Cooper (1960) demonstrated yeast preferences among larvae of *D. pseudoobscura* and *D. persimilis*, the preference varying according to the combination of yeasts offered.

In the neotropical forest, Heed (1957) showed that net sweeping over a variety of fallen fruits and blossoms yields a large aggregation of species belonging to the family Drosophilidae, feeding on the micro-organisms growing on these plant parts. Most are members of the genus *Drosophila*, but eight species of the genus *Clastopteromyia* and three of *Neotanygastrella* were found in the same aggregation. A second facies of the forest supports certain flower-feeding species of *Drosophila*, adults of which both feed and breed in living (not fallen) flowers (Pipkin, 1964). Flower feeders are seldom collected by net sweeping over the forest floor. A third facies includes species of the genus *Zygothrica* and of several subgenera of *Drosophila* that feed on fungi and breed either in these fungi or in living flowers. The present work is concerned with the influence of adult and larval food habits on population size in ground-feeding Drosophilidae of the first facies and on estimates of the sizes of natural population samples of different species.

METHODS

Flies were collected by trapping, net sweeping, and breeding from plant parts. Traps consisted of two five-gallon lard cans with

the end removed, baited with banana, pineapple, and orange, suspended about 3 feet off the ground and 10 feet apart. The fruits acquired growth of indigenous yeasts within a few days. Contents of traps were buried once a week when collections were made, and fresh bait was introduced. Sweeping collections were made with a short-handled net, the flies being transferred directly to vials containing culture medium. Flies were bred from various fallen blossoms, fruits, stems, and from flowers broken off the living plants. Quart Mason jars were used for drier plant parts, and flower pots of the same capacity for juicy fruits. Each container was approximately half filled with plant parts from a single collection site so as to provide a roughly equal volume of plant material in each.

Forest collections using all three methods were made in two principal areas; Barro Colorado Island, Canal Zone, altitude 279 feet, and at two stations at Cerro Campana, R. P., at altitudes of 2200 and 2500 feet. Regular collections were made each week between 9 and 10:30 AM. Occasional collections were made between 11 AM
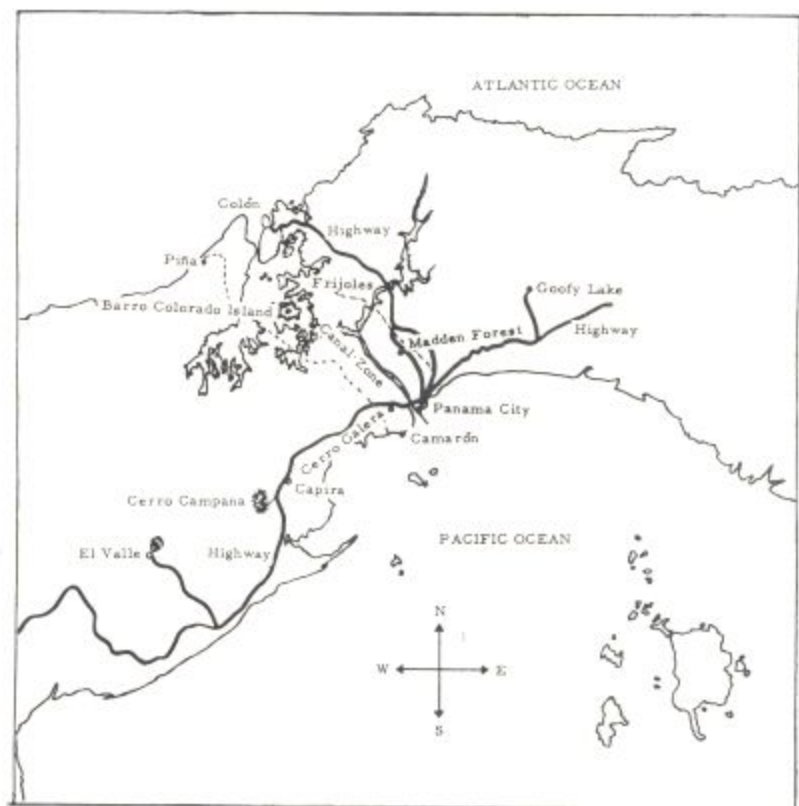

Fig. 1.—Map showing location of collecting areas in central Panama.

and 2 PM to determine adult resting places. Each sweeping collection was taken from a single micropopulation, feeding on fallen fruit or blossoms in a restricted area, usually from a single tree, vine, or other plant. Collections at Barro Colorado Island were made along the Barbour Lathrop, Snyder Molino, and W. M. Wheeler Trails. The lower collecting area at Cerro Campana was the forested hillside at the base of the great cliff; the higher area included forest adjacent to a small coffee finca. Other net sweeping and plant part breeding collections were made in the following areas (see map, Fig. 1): Madden Forest, Canal Zone; forest of the Piña region, Ft. Sherman Reservation, Canal Zone; forests near Goofy Lake and El Valle, R. P., and fincas near Frijoles, Canal Zone; Capira and Camaron, R. P. The following forest locations were also visited for collections in other parts of Panama: Almirante, Bocas del Toro Province; El Volcán, Chiriqui Province; El Real, Darien Province. Collections in central Panama were begun September, 1959 and continued until March, 1962. Collections in other parts of Panama were undertaken in 1962 and 1963.

RESULTS AND CONCLUSIONS
ADULT FEEDING ASSOCIATIONS

The present study groups the species of ground-feeding Drosophilidae into three overlapping classes according to adult and larval plant preferences and readiness to enter traps baited with cultivated fruits. Class "A" species prefer small drier fallen fruits and blossoms both for adult feeding and larval breeding; they enter traps to a limited degree. Class "B" species use fleshy fruits in addition to the drier fruits both for feeding and breeding and enter traps to a moderate extent. Fleshy fruits as well as the small drier fruits serve Class "C" species for breeding, and these species show a strong inclination to enter traps.

Table 1 lists 34 species of Drosophilidae which may be netted together in class A feeding aggregations. No species occurring in fewer than 10 collections are included in the table. Usually between 10 and 20 class A species were netted in a single micropopulation. These aggregations remained intact at midday resting places under dead leaves, especially in the dry season when moist areas were sought. Of these species, 61.1% belong to the *Drosophila* tripunctata species group, 15.9% to the *Drosophila* dreyfusi, canalinea, and calloptera species groups, and 18.2% to the genus *Clastopteromyia*.

Table 1 also gives the percentages with which ground-feeders of class A were trapped or netted in 170 paired collections at Barro Colorado Island and Cerro Campana during the two and a half years collection period. A paired collection comprises one net sweeping and one trapping collection of the same day at either of the two major stations. These percentages show that most class A ground-feeders seldom come to traps baited with cultivated fruits, although the species vary in this respect. This behavior reflects a preference

TABLE 1.—Class A (ground-feeding) Drosophilidae: Relative frequency of 34 species in 170 paired trap and net-sweeping collections at Barro Colorado Island and Cerro Campana

Species	No. trap coll.	% total trap coll.	No. net coll.	% total net coll.
Drosophila (Drosophila)				
Tripunctata group				
Subgroup I				
angustibucca	3	1.8	68	40.0
mediocris	1	0.6	51	30.0
setula	26	15.3	51	30.0
Subgroup II				
medionotata	12	7.1	98	57.6
unipunctata	0	0	19	11.2
roehrae	2	1.2	30	17.6
Subgroup III				
blumelae	1	0.6	18	10.6
johnstonae	1	0.6	13	7.6
bodemannae	0	0	13	7.6
converga	0	0	51	30.0
fragilis	1	0.6	10	5.9
mediopicta	10	5.9	12	7.1
mediopictoides	34	20.0	30	17.6
mediostriata	20	11.8	82	48.2
nigricincta	1	0.6	14	8.2
trapeza	8	4.7	11	6.5
Subgroup IV				
albirostris	0	0	64	37.6
medioparva	1	0.6	23	13.5
"medioparva-like"	0	0	11	6.5
metzii	0	0	18	10.6
Ungrouped				
argenteifrons	1	0.6	27	15.9
Canalinea group				
canalinea } canalinioides	0	0	12	7.1
Calloptera group				
calloptera	0	0	47	27.6
schildi	0	0	19	11.2
Drosophila (Sophophora)				
Willistoni group				
fumipennis	1	0.6	102	60.0
Clastopteromyia				
albinota	0	0	28	16.5
opaca	0	0	23	13.5
species "A"	0	0	17	10.0
species "B"	0	0	20	11.8
species "C"	0	0	10	5.9
species "D"	0	0	16	9.4
species "E"	2	1.2	23	13.5
species "F"	0	0	30	17.6

for wild fruits for oviposition and/or feeding, not a dislike for flying off the forest floor; many of these species also oviposit in flowers growing 6 feet or more from the floor.

A list of eight class B ground-feeders and 18 class C species appears in Table 2; several rarely collected species are omitted. Class

TABLE 2.—Classes B and C (ground-feeding) Drosophilidae: Relative frequency of 26 species in 170 paired trap and net sweeping collections at Barro Colorado Island and Cerro Campana

	No. trap coll.	% total trap coll.	No. net coll.	% total net coll.
Class B				
Drosophila (Drosophila)				
Repleta group				
moju	17	10.0	7	4.1
Drosophila (Sophophora)				
Willistoni group				
capricorni	9	5.3	18	10.6
nebulosa	10	5.9	35	20.6
sucinea	31	18.2	37	21.8
equinoxalis				
tropicalis	118	69.4	116	68.2
paulistorum				
willistoni				
Class C				
Drosophila (Drosophila)				
Cardini group				
cardini	32	18.8	7	4.1
cardinoides	69	40.6	37	21.8
neomorpha	89	52.4	29	17.1
Repleta group				
fulvimacula	64	37.6	9	5.3
eohydei	27	15.9	2	1.2
paranaensis	73	42.9	4	2.4
repleta	48	28.2	2	1.2
fasciola	28	16.5	5	2.9
Pallidipennis group				
pallidipennis	21	12.4	1	0.6
Drosophila (Sophophora)				
Melanogaster group				
ananassae	88	51.8	8	4.7
melanogaster	106	62.3	14	8.2
simulans	71	41.8	16	9.4
Saltans group				
sturtevanti	138	81.1	19	11.2
emarginata	63	37.1	2	1.2
prosaltans	33	19.4	2	1.2
Drosophila (Pholadoris)				
latifasciaeformis	93	54.7	7	4.1
Neotanygastrella				
chymomyzoides	42	24.7	5	2.9
"chymomyzoides-like"	28	16.5	3	1.8

B species are frequently found feeding in the same aggregations with class A species over fallen blossoms and drier fruits. They show a moderate or no aversion to entering traps. In contrast with species of classes A or B, members of class C are rarely found hovering over small drier fallen fruits and blossoms, but they are easily attracted to traps. Class C species may feed not only on juicy fruits, where they certainly breed, but also in sites above the level of the forest floor, such as in slime fluxes of trees. Carson *et al.* (1956) found that *D. pseudoobscura* and *D. persimilis*, trap attractable species of the western United States, do indeed possess different adult feeding and larval breeding sites.

LOCAL VARIATIONS IN DISTRIBUTION OF SPECIES

The species content of aggregations collected by net sweeping was generally similar in different forested areas but there were some localizations of particular species. For example, *D. albirostris* and *D. metzii* were collected regularly at every station except Cerro Campana. Both species were taken at Turrialba, Costa Rica, at the same altitude as the lower collecting area at Cerro Campana. Their absence from the latter station must not be related to altitude. Many of the common food plants for these *Drosophila* species are the same at Cerro Campana as at Barro Colorado Island.

Although most trap-attractable species were similar at Cerro Campana and Barro Colorado Island, *D. emarginata*, common throughout the collecting period at Cerro Campana, was trapped only once at Barro Colorado Island. *Drosophila eohydei* and *D. pallidipennis* were trapped regularly at Cerro Campana, but the former species never, the latter only twice at Barro Colorado Island.

ADULT FEEDING SOURCES

Flies of class A Drosophilidae have been observed actively feeding on fallen fruit or blossoms of a large variety of plants. However, it is not certain whether every female collected by net sweeping over fallen fruit was feeding, ovipositing, or both. *Drosophila angustibucca* was netted from fallen fruit or blossoms of 36 different plant species, as follows: fruits of an undescribed *Clusia* sp. (figs); *Erythrina berteroana* (gallito); *Andira inermis* (cabbagebark); *Calocarpum viride* (mamey); *Theobroma cacao* (cocoa); *Coffea arabica* (coffee); *Guilielma gasipaes* (pejibaye palm); *Spondias mombin* (hogplum); *Bactris* sp. (black palm); *Crysophila warscewiczii* (fan palm); drupe 25, 115, nuts 53, 83, 120, 144; fruits 9, 11, 36, 37, 39, 42, 54, 66, 114 117, 119, 130, 140, 210; blossoms of *Bombax barrigon, Musa sapientum* (banana); blossoms 33, 67; sprouting nuts 1; buds 211. The unidentified fruits, listed by number, were small, with thin rinds, and all except the drupes were of the drier type. *Drosophila mediocris* and *D. albirostris* were netted from parts of 31 and 32 different plant species, respectively, *D. medionotata* from parts of 64.

Common species of classes B and C were netted from fallen

plant parts of fewer plant species than were the common species of class A. For example, *D. nebulosa* of class B, was taken from 13 species: fruits of *Chrysophyllum cainito, Coffea arabica, Theobroma cacao, Clusia* sp., *Andira inermis, Spondias mombin, Mangifera indica* (mango), *Bactris* sp., *Guilielma gasipaes,* fruit 3, nuts 53; blossoms of *Bombax barrigon,* blossoms 33. *Drosophila sturtevanti* of class C, was netted from 10 plant species: fruits of *Theobroma cacao, Clusia* sp., *Andira inermis, Spondias mombin, Bactris* sp., *Guilielma gasipaes, Musa sapientum, Calocarpum viride,* fruit 5, and blossoms of *Bombax barrigon. Drosophila cardinoides,* class C, was netted from fallen parts of 14 plant species: fruits of *Chrysophyllum cainito, Theobroma cacao, Clusia* sp., *Andira inermis, Spondias mombin, Guilielma gasipaes, Musa sapientum,* fruit 117, 60, 42; blossoms of *Bombax barrigon, Grias pittieri, Beaumontia grandiflora,*

TABLE 3.—Plants used by larval *Drosophila* of classes
A, B, and C as breeding sources

Drosophila class A	Fallen fruit or blossom	Living flower
medioparva	*Coffea arabica, Crysophila warscewiczii, Siparuna nicaraguensis,* blossom of *Crecropia mexicana.*	*Calathea macrosepala, Aphelandra micans, Centropogon coccineus,* Aroid sp.
medionotata	*Calocarpum viride, Coffea arabica, Clusia* sp., *Andira inermis, Siparuna nicaraguensis,* drupe 115, fleshy fruit 118, gourd 48C; blossoms of *Bombax barrigon,* of *Erythrina berteroana,* of woody vine 3VC.	*Costus* sp. *Helianthus* sp.
angustibucca	*Clusia* sp., *Andira inermis, Crysophila warscewiczii,* drupe 151 pod of *Erythrina berteroana,* blossom of *Erythrina berteroana*	
Drosophila class B		
nebulosa	*Mangifera indica, Clusia* sp., *Carludovicia palmata, Andira inermis, Chrysophyllum cainito*	
sucinea	*Coffea arabica, Clusia* sp., drupe 115, fleshy fruit 118, fleshy fruit 119.	
Drosophila class C		

blossoms 197. Fruits over which species of classes B and C were found were, in general, more fleshy than those supporting members of class A, though there is some overlapping.

LARVAL AND PUPAL DEVELOPMENT SOURCES

Table 3 presents a list of plants whose fallen fruits or blossoms serve for larval development of *Drosophila* of the three classes. The fallen plant parts over which adults of all three classes were collected by sweeping were similar to those occupied by their respective larvae and pupae. Table 3 shows that members of all three classes also underwent larval and pupal development in flowers still attached to their plants. Since these living flowers also have been found serving two undescribed species of the genus *Clastopteromyia* and several species of *Zygothrica* (adults of which feed on fungi), this type of breeding site may represent a primitive characteristic for Drosophilidae.

Plant parts in which larvae and pupae are developing may serve also for the feeding of adults. The variety of species collected by sweeping over a given plant part includes many of those bred from a sample of the same material. For example, Table 4 shows that six of the eight species of *Drosophila* hatching from a single sample of fallen fruit of *Andira inermis* were included in the 13 species of *Drosophila* and *Clastopteromyia* caught by net sweeping at the same time and place. The number of flies hatching in the five time intervals

TABLE 3.—(continued)

sturtevanti	*Mangifera indica,* *Guilielma gasipaes,* *Andira inermis,* *Annona muricata.*	
melanogaster	*Mangifera indica,* *Clusia* sp., *Bactris* sp., *Andira inermis,* *Artocarpus communis.*	*Hedychium coronarium.*
ananassae	*Cocos nucifera,* *Mangifera indica.* *Bactris* sp., *Artocarpus communis,* *Clusia* sp., *Andira inermis,* gourd 193.	*Hedychium coronarium,* *Calathea violaceae,* domestic tubular flower 6D.
cardinoides	*Annona muricata,* *Clusia* sp., *Andira inermis,* small mushrooms 5MF, Aroid sp. 45C, vine blossoms 3VC.	*Heliconia latispatha,* *Hedychium coronarium,* *Calathea violaceae.*
neomorpha	*Coffea arabica, Clusia* sp., *Guilielma gasipaes,* *Andira inermis,* *Siparuna nicaraguensis,* Aroid sp. 45C, berries 149.	*Aphelandra micans*

listed in Table 4 demonstrates that *D. converga, D. sturtevanti, D. nebulosa, D. cardinoides, D. tropicalis,* and *D. equinoxalis* were undergoing almost synchronous larval and pupal development. In a large fleshy fruit, *Annona muricata* (soursop), on the other hand, successional development has been observed. In a further example, from fallen fruit of a single sample of a *Clusia* sp., four of the five hatching species were previously netted with 12 additional species. A number of similar collections have corroborated the finding that many of the species collected as adults over fallen plant material can be bred from a sample of the same plant.

Although fallen fruits or blossoms with no adults apparent at the time of collection might later yield hatching flies, usually an aggregation of flies was found hovering over the fallen plant parts. Where an aggregation of Drosophilidae was found feeding, the number of species netted was generally greater than the number of species bred out of a sample of plant parts. Out of 21 paired sweeping and breeding collections where six or more species were netted, in only 4 cases were as many species bred from a limited volume of plant parts as were netted. In six cases, there were twice as many species netted as hatched, and in the remaining 11 samples, from 3 to 11 times as many.

The higher number of species collected by sweeping is partly due to the fact that a few of the netted species were feeders only and bred elsewhere. For example, although eight common species of *Clastopteromyia* regularly feed with other class A members, only

TABLE 4.—Comparison of species netted over fallen fruit of *Andira inermis* with those hatching from a sample of the same fruit collected at the same time (Feb. 1) that flies were netted

| Species Drosophila | No. flies netted | No. flies hatching | | | | | Total nos. | % total hatching |
		Feb. 14	Feb. 16	Feb. 20	Feb. 24	Feb. 26		
tropicalis	84	292	709	343	206	343	1893	94.0
equinoxalis								
nebulosa	1	2	0	1	4	14	21	1.0
melanogaster	0	2	0	0	1	4	7	03.
cardinoides	2	3	6	7	0	0	16	0.8
neomorpha	1	1	4	4	0	0	9	0.5
sturtevanti	1	0	0	23	25	14	62	3.1
angustibucca	0	0	0	2	0	0	2	0.1
converga	1	0	3	0	0	0	3	0.2
mediostriata	1							
albirostris	1							
mediocris	1							
medionotata	2							
fumipennis	2							
Clastopteromyia								
albinota	1							
sp.	3							

one has ever been bred from a fallen fruit (*Clusia* sp.). The breeding locations of the seven other common members of this genus are unknown, but two rare species have been bred from living flowers. Table 4 shows that two species of *Clastopteromyia* were netted but not bred from the fruit of *Andira inermis*.

Conversely, some species of *Drosophila* that both feed and breed in living flowers can be hatched from fallen blossoms, but are rarely collected as adults by netting over fallen plant parts; e.g., "gray bromeliae," an undescribed member of the flavopilosa group and *D. sticta* (see Table 5). Eggs of these species were presumably deposited while the blossoms were still attached to the plant, and therefore were among the first to hatch.

A single sample of fallen plant part will yield fewer *Drosophila* species hatching than netted, but if the hatching results of a number of samples of fruit of the same plant species are combined, then many of the netted species can be bred out of the combined samples. For example, from six collections of *Clusia* sp. fruit at Barro Colorado Island and Cerro Campana, seven class A species (*D. fumipennis, D. converga, D. angustibucca, D. metzii, D. mediostriata, D. albirostris, D. medionotata*) and two class B species (*D. tropicalis* and *D. equinoxalis*) were both netted in a single collection and bred from at least one of the six *Clusia* fruit collections.

The consistency with which the species netted outnumber the species bred from samples of the same plant parts indicates that a spatial interference of ovipositing females occurs, similar to the intraspecies interference with oviposition observed by Pearl (1932) in crowded culture bottles of *D. melanogaster*. The feeding and ovipositing aggregation is made up of small numbers of individuals of

TABLE 5.—Comparison of species netted over fallen pea family vine blossoms with those hatching from a sample of the same blossoms collected at the same time (Dec. 13) that flies were netted

Species *Drosophila*	No. flies netted	No. flies hatching			Total hatching
		Dec. 27	Dec. 29	Dec. 31	
"gray bromeliae"	0	33	3	2	38
sticta	0	1	2	0	3
converga	0	5	2	0	7
cardinoides	0	11	1	0	12
albirostris	6	4	1	1	6
mediostriata	3	8	24	7	39
metzii	1	1	0	0	1
crocina	4	18	20	2	40
mediopatva	1				
medionotata	1				
fumipennis	2				
latifasciaeformis	1				
Clastopteromyia					
sp.	1				

many species; the result could be a spatial interference between females of different species.

Closely related *Drosophila* species are cohabiting with respect to larval development. Table 4 shows that *D. cardinoides* and *D. neomorpha*, both members of the cardini group, were hatched on the same day from fruit of *Andira inermis*. Similarly, Table 5 shows five members of the tripunctata group, namely, *D. crocina, D. converga, D. albirostris, D. mediostriata*, and *D. metzii*, undergoing nearly synchronous development in fallen vine blossoms. Table 6 lists other examples of members of the same species group that underwent larval development in the same sample of the same plant part and hatched on the same day. Included are two pairs of sibling species (*D. melanogaster* and *D. simulans; D. johnstonae* and *D. blumelae*).

Indirect evidence that fallen plant parts are used for adult feeding as well as for oviposition is furnished by the secondary sex ratio of species netted, contrasted with that in the same species trapped. An especially low percentage of males in a trap collection compared

TABLE 6.—Related *Drosophila* species undergoing nearly synchronous larval and pupal development in the same sample of the same plant part

Drosophila (*Drosophila*) Tripunctata group	fallen plant part (fruit or blossom)	Cardini group	fallen plant part (fruit or blossom)
medionotata, medioparva	*Coffea arabica*	*neomorpha, cardinoides*	*Clusia* sp. *Andira inermis* Aroid 45C
johnstonae blumelae	sprouting nuts 1	*cardini, cardinoides*	*Clusia* sp. *Andira inermis*
angustibucca mediocris mediostriata medionotata	*Clusia* sp.	*Drosophila* (*Sophophora*) Melanogaster group	
bodemannae angustibucca	*Erythrina berteroana* (blossoms)	*melanogaster, ananassae*	*Bactris* sp., *Artocarpus communis*
argenteifrons albirostris medionotata converga	*Clusia* sp.	*ananassae, simulans*	*Theobroma cacao*
metzii, greerae, albirostris, medionotata	*Bombax barrigon* (blossoms)	*melanogaster, simulans*	*Mangifera indica*
Repleta group *fulvimacula, fasciola*	*Coffea arabica,* "guanarana" 42C	Willistoni group *nebulosa, willistoni* siblings	*Annona muricata*
		Saltans group *prosaltans, sturtevanti*	*Annona muricata*

with that in a sweeping collection may indicate a special preference of the females for the fleshy fruit of the trap bait for egg laying.

Several factors affect the secondary sex ratio equally in both netted and trapped collections. These include greater female longevity (Pipkin, 1956), greater resistance of females to a *Treponema* infection (Sakaguchi and Poulson, 1960), and genetic sex ratio mechanisms (Gershenson, 1929; Darlington and Dobzhansky, 1942). Because females begin to hatch earlier than males in *Drosophila*, the sex ratio of a single large collection where flies are hatching may depend on whether hatching has just begun or is well advanced. Hence observed sex ratios in a large number of minimal populations provide more reliable information than do sex ratios of expanded populations, where the proportion of males to females is altered by the age (relative to hatching) of the population. Minimal populations are here defined as those that include 14 or fewer flies; expanded populations, those including 15 or more flies.

The cases most clearly suggesting that females prefer to oviposit on the cultivated fruits of the traps are *D. capricorni, D. cardinoides*, and the willistoni sibling species (Table 7). Here minimal populations

TABLE 7.—Secondary sex ratio (δ / φ) in minimal and expanded populations of neotropical *Drosophila*

Class A	minimal trapped	minimal netted	expanded netted	expanded trapped
mediocris	0.42	..	..	..
mediostriata	0.80	..	0.98	..
medionotata	0.79	..	0.54	..
albirostris	1.20	..	1.62	..
angustibucca	0.72	..	0.83	..
calloptera	1.20	..	1.62	..
fumipennis	1.14	..	1.33	..
Class B				
capricorni	0.54*	0.15	0.45	0.13
nebulosa	1.15	..	1.37	..
"willistoni siblings"	0.69*	0.55	1.09	0.48
moju	1.50	..	1.07	..
Class C				
ananassae	0.47	2.00	1.05	1.58
sturtevanti	0.76	0.64	0.61	0.64
emarginata	..	0.76	..	0.78
prosaltans	..	1.13	..	..
cardinoides	1.17*	0.66	0.33	1.18
neomorpha	0.59	0.46	1.88	0.77
repleta	..	1.02	..	..
fulvimacula	..	0.68	..	1.01
fasciola	..	1.14	..	..
latifasciaeformis	0.96	0.99	1.49	0.86

* Sex ratios of minimal trapped collections are significantly lower than sex ratios of minimal netted collections.

collected by trapping have a significantly higher proportion of females than minimal netted populations. Chi square tests for independence comparing numbers of males and females in minimal trapped versus netted populations of *D. capricorni*, *D. cardinoides*, and the willistoni siblings, all yield P-values less than .01. For *D. neomorpha*, *D. nebulosa*, and *D. sturtevanti*, the ratios of males to females in minimal netted collections do not differ significantly from those in minimal trapped collections.

An unusual excess of males in minimal trapped collections of *D. ananassae* and an excess of females in minimal netted populations may be attributed to the female's preference for wild fruits for oviposition rather than for cultivated trap bait (chi square 9.37; $P < 0.01$).

VARIATION IN MEAN SIZE OF SWEEPING AND TRAPPING COLLECTIONS

Table 8 gives mean numbers of flies per sweeping collection both in minimal and expanded population samples for class A ground-feeders. Although minimal population samples may include as many

TABLE 8.—Mean sample size of minimal and expanded populations of class A species collected by net sweeping

Drosophila	Mean no. flies per minimal net. coll.	No. minimal net coll.	Mean no. flies per expanded net coll.	No. expanded net coll.
medioparva	1.86 ± 0.28	28	....	0
mesostigma	1.88 ± 0.39	16	55.0	1
mediocris	1.96 ± 0.14	76	....	0
trapeza	2.06 ± 0.34	18	....	0
fragilis	2.16 ± 0.44	17	19.5	2
greerae	2.37 ± 0.72	19	....	0
crocina	2.42 ± 0.53	12	34.0	1
blumelae	2.55 ± 0.46	29	19.0	4
nigricincta	2.73 ± 0.78	15	....	0
metzii	2.74 ± 0.43	31	20.0	2
setula	2.94 ± 0.28	71	49.9	8
mediopictoides	2.94 ± 0.47	34	54.3	3
converga	3.12 ± 0.34	68	43.6	16
medionotata	3.13 ± 0.23	152	23.8	10
johnstonae	3.27 ± 0.67	15	18.3	3
albirostris	3.39 ± 0.26	104	30.1	8
mediopicta	3.47 ± 0.82	15	82.0	1
angustibucca	3.51 ± 0.34	96	27.1	14
argenteifrons	3.61 ± 0.60	36	24.3	3
mediostriata	3.96 ± 0.32	106	43.2	38
bodemannae	4.38 ± 1.17	16	....	0
fumipennis	3.96 ± 0.27	144	39.9	34
schildi	3.62 ± 0.40	39	22.0	1
calloptera	4.39 ± 0.45	72	22.4	8

as 14 individuals, the greatest average minimal population size among 24 class A species was only 4.39 ± 0.45 (mean $\pm$ SE) flies per collection (*D. calloptera*). A comparison of means of minimal samples in Table 8 shows significant differences between *D. medioparva* and *D. setula* (Diff $\pm$ SED $= 1.08 \pm 0.41$) and also between *D. mediocris* and *D. setula* (0.98 ± 0.32). Means in excess of that of *D. setula* were likewise significantly higher than those of *D. medioparva* and *D. mediocris* where the number of collections was adequate for comparison. The mean minimal sample size both of *D. setula* and *D. medionotata* was significantly lower than that of *D. mediostriata* (Diff $\pm$ SED, 1.02 ± 0.44 and 0.83 ± 0.41, respectively). Similarly, mean sample size of *D. converga* was significantly lower than that both of *D. calloptera* and *D. fumipennis* (1.27 ± 0.56 and 0.84 ± 0.43, respectively). Finally, the mean sample size of *D. albirostris* was significantly lower than that of *D. calloptera* (1.00 ± 0.51). Relative population sizes are of interest because when natural selection is acting on feeding and ovipositing drosophilids, the flies are dispersed in aggregations composed of a number of species, each represented by few individuals.

Means of samples of expanded populations of class A species ranged from 19.0 individuals (*D. blumelae*) to 49.9 individuals per collection (*D. setula*), considering only species in which expansions were encountered four or more times. Expanded populations were found fewer than four times in 14 of 24 class A species; in six of these fourteen (*D. mediocris, D. medioparva, D. bodemannae, D. trapeza, D. greerae,* and *D. nigricincta*) not a single expanded population was collected, although minimal populations were found regularly.

The five species found most frequently in minimal populations include *D. fumipennis, D. medionotata, D. mediostriata, D. angustibucca,* and *D. albirostris,* which were taken between 96 and 146 times. With the exception of *D. albirostris,* which gave place to *D. converga,* these same species were also most frequently taken (from 10 to 38 times) in expanded populations.

Table 9 presents the mean number of individuals in minimal and expanded samples collected by netting and by trapping for four class B and 17 class C species. A comparison of means of minimal samples shows the trap mean to be significantly higher than the sweeping mean for only two species, *D. sturtevanti* (Diff $\pm$ SED $= 2.20 \pm 0.91$) and *D. cardinoides* (2.21 ± 0.65). Mean sample sizes of *D. capricorni, D. fulvimacula,* and *D. latifasciaeformis* were slightly higher in minimal trapping than in minimal sweeping collections, but significant differences could not be demonstrated in cases where the number of collections by either method was low. In contrast, the mean number of individuals of *D. nebulosa* and of *D. moju* was slightly higher in netted than in trapped minimal collections.

The sizes of expanded samples of class C species were somewhat higher in trapped than in netted collections or differed little. This may indicate attraction to the trap bait from a slightly larger area

TABLE 9.—Mean sample of minimal and expanded populations of class B and C species collected either by net sweeping or by trapping or by both methods

Drosophila Class B	Mean no. flies per minimal net coll.	No. minimal net coll.	Mean no. flies per expanded net coll.	No. expanded net coll.	Mean no. flies per minimal trap coll.	No. minimal trap coll.	Mean no. flies per expanded trap coll	No. expanded trap coll.
capricorni	3.22 ± 0.65	27	28.7	3	4.00	15	41.8	+
nebulosa	3.76 ± 0.44	41	39.6	8	2.00	11	......	:
sucinea	3.98 ± 0.47	50	92.7	13	4.00 ± 0.36	29	50.3	+
moju	5.00	12	77.5	6	1.71	17	19.0	1
Class C								
ananassae	2.73	11	38.0	6	3.78 ± 0.44	58	47.1	35
melanogaster	2.53(♂)	15	62.2	5	2.79 ± 0.31(♂)	43	67.2(♂)	49
simulans	3.11(♂)	19	28.5	4	2.52 ± 0.28(♂)	46	88.1(♂)	26
sturtevanti	3.96 ± 0.74	24	92.7	14	6.16 ± 0.61	43	125.9	130
emarginata	4.75	4	......	:	5.19 ± 0.71	31	97.8	59
prosaltans	1.25	4	......	:	1.76 ± 0.17	37	17.0	1
cardini	3.11	9	......	:	3.41 ± 0.50	34	59.0	2
cardinoides	2.50 ± 0.37	46	24.3	3	4.71 ± 0.54	48	41.6	23
neomorpha	3.16 ± 0.41	57	28.0	1	3.91 ± 0.42	74	39.8	6
repleta	1.00	2	......	:	2.14 ± 0.27	49	......	:
fulvimacula	2.82	11	22.5	2	3.94 ± 0.42	64	37.9	7
eohydei	1.50	4	......	:	2.50 ± 0.44	28	......	:
fasciola	2.62	13	......	:	2.12 ± 0.33	34	......	:
pallidipennis	1.00	1	86.0	1	2.59 ± 0.58	22	74.2	6
latifasciaeformis	3.18	17	100.7	6	4.84 ± 0.45	61	42.1	33
Neotanygastrella								
chymomyzoides	2.75 ± 0.71	20	20.5	4	3.50 ± 0.49	38	22.0	1
"chymomyzoides-like"	1.33	3	......	:	2.27 ± 0.34	30	38.0	1

than to the natural feeding or breeding source. On the other hand, mean sizes of expanded samples of class B species *D. nebulosa*, *D. sucinea*, and *D. moju* were higher in netted than in trapped collections, showing a disinclination for entering traps in large numbers. Mean minimal sample sizes of between two and four flies per collection accounted for 61.9% of class B and C species in Table 9, as measured by trapping collections and 79.2% of the class A species of Table 8, as measured by sweeping collections. Therefore, minimal sample sizes of species of all three classes are similar, although class A samples were collected by sweeping and classes B and C by trapping. This indicates that all ground-feeding *Drosophila* can be scattered as numerically small portions of multispecific feeding and/or ovipositing aggregations.

Expanded populations are more frequent in class B and C species than in class A species in general. Thus, from 16 to 33% of the total netted collections of three class B species, *D. nebulosa*, *D. sucinea*, and *D. moju*, represented expanded populations. Similarly, four class C species, *D. ananassae*, *D. melanogaster*, *D. simulans*, and *D. sturtevanti*, were collected as expanded populations in from 17 to 37% of the total netted collections of these species. However, of 24 class A species listed in Table 8, only *D. fumipennis* and *D. mediostriata* were found as expanded populations in as many as 19% and 26%, respectively, of the total number of netted collections. Since expanded populations are often hatching from a breeding source, this difference is partly dependent on the fact that class B and class C species utilize large fleshy fruits, whereas class A species prefer the smaller drier fruits and blossoms.

Willistoni sibling species of five netted collections taken from fruits of three forest trees (*Andira inermis*, *Clusia* sp., *Bactris* sp.) and four trap collections, all collected from Barro Colorado Island over a period of 18 months, were identified by Mr. B. Spassky. His analysis,

TABLE 10.—Numbers of the "willistoni sibling" species identified from collections made during eighteen months at Barro Colorado Island

Net coll.	*tropicalis*	*equinoxalis*	*willistoni*	*paulistorum*
16B4	5	9	1	0
17B1	9	10	1	2
23B9	15	48	18	0
49B2	47	26	12	0
55B6	28	9	2	0
Total	104	102	34	2
%	43.0	42.1	14.1	0.8
Trap coll.				
16B8	5	4	0	0
49B22	10	45	1	0
54B3	21	3	0	0
88B1	33	42	4	0
Total	69	94	5	0
%	41.0	56.0	3.0	0

based on examination of male progeny of single females collected in nature, appears in Table 10. The dominant species of this sibling set are *D. tropicalis* and *D. equinoxalis*, occurring with roughly equal frequency.

Assuming that proportions of these two species remained the same in this area during the collection period, estimates can be made of their sample sizes. Letting minimal samples be represented by 28 and fewer individuals, the average number of flies per sample in 52 minimal collections of the willistoni siblings was 8.85. The mean number of flies per expanded sample in 47 netted collections was 62.0. Neglecting the frequencies of *D. paulistorum* and *D. willistoni*, we may halve the estimates, obtaining 4.4 flies per minimal and 31.0 flies per expanded netted collection for either *D. tropicalis* or *D. equinoxalis;* these figures closely resemble the corresponding sweeping sample sizes of other willistoni group members, *D. capricorni, D. nebulosa,* and *D. sucinea.*

For the willistoni sibling species, the average number of flies per minimal trapped sample was 10.4; per expanded trapped sample, 252.2. Assuming that the two dominant species show a similar attractivity to traps, these figures may be halved, giving estimates of 5.2 flies per minimal trapped sample and 126.1 flies per expanded sample. The former estimate is closely similar to that of other class B species, but the latter is four times the estimate of the mean of expanded netted samples. This suggests either that attractivity to

TABLE 11.—Relative size of hatching population samples

Drosophila	No. coll. bred	Mean no. flies hatching per pint of plant part
Class A		
medioparva	11	2.36
angustibucca	7	2.40
albirostris	16	3.18
converga	5	4.60
medionotata	17	5.80
metzii	9	5.40
mediostriata	12	11.42
Class B		
nebulosa	9	7.40
sucinea	5	12.20
"willistoni siblings"	44	109.95
Class C		
cardinoides	20	6.65
neomorpha	14	11.43
sturtevanti	10	22.10
ananassae	11	43.82
melanogaster (♂)	9	13.11
simulans (♂)	7	2.14
fasciola	7	3.57
fulvimacula	4	24.25

trap bait was stronger than to a natural feeding and breeding source or that flies were drawn from a larger area to a trap than to a natural fruit pile.

VARIATION IN SIZE OF SAMPLES HATCHING FROM PLANT PARTS

The average size of hatching populations of various drosophilids of classes A, B, and C may be seen in Table 11. These means are derived from the number of flies hatching per quart container half filled with plant material. Since a number of different fallen fruits and blossoms and some living (not fallen) flowers were used to breed these populations, no pretense is made that the mean number of each species hatching is derived from exactly equal volumes of plant parts. Nevertheless, Table 11 demonstrates that class A species in general produced fewer individuals per sample of plant parts than did most class B and C species. This is in agreement with studies of adult populations collected by netting or trapping. The size of *D. mediostriata* hatching populations was approximately double or more that of any other tripunctata group member, an expected corollary of the observation that this species expands its populations more frequently than others of the group.

Not all class C species hatched in large populations. For example, *D. fasciola* hatched in small populations (Table 11) and only small populations were collected either by sweeping or by trapping (Table 9). The hatching populations of the willistoni siblings include four species, of which *D. tropicalis* and *D. equinoxalis* are the dominant members and are about equally represented. Thus the hatching population size of each of the latter two species is of the same order of magnitude as that of *D. ananassae*. Means of *D. melanogaster* and *D. simulans* are derived from males only and should be doubled to be comparable with those of the other species in Table 11. A comparison of the mean number of flies hatching from a pint of plant material (Table 11) with the mean number of flies obtained in a single sweeping or trapping collection (Tables 8 and 9) shows that only a very small fraction of flies hatched in nature is caught by these methods in single micropopulations.

FLUCTUATIONS IN POPULATION NUMBERS

Fluctuations in numbers of individuals of various species were determined for a single locality each, either Barro Colorado Island or Cerro Campana, using either sweeping or trapping. Monthly percentages for each species were calculated according to the method of Patterson (1943).

Fluctuations of population numbers showed three main patterns: (1) species with expansions during one or more months of the wet season (Fig. 2) or (2) of the dry season (Fig. 3), and (3) those with expansions either in alternate months, irregular, or lacking (Fig. 4).

In central Panama the wet season extends from May through December. Intermittent rains occur to mid-January on the Pacific side of the isthmus and usually throughout the dry period on the Atlantic side. Mean diurnal temperature of the forest floor at Barro Colorado Island, based on a limited record, is near 21 C, with little variation (Kenoyer, 1929). Mean monthly fluctuation is less than 1° C. The dry season is a time of flowering and fruiting for many trees,
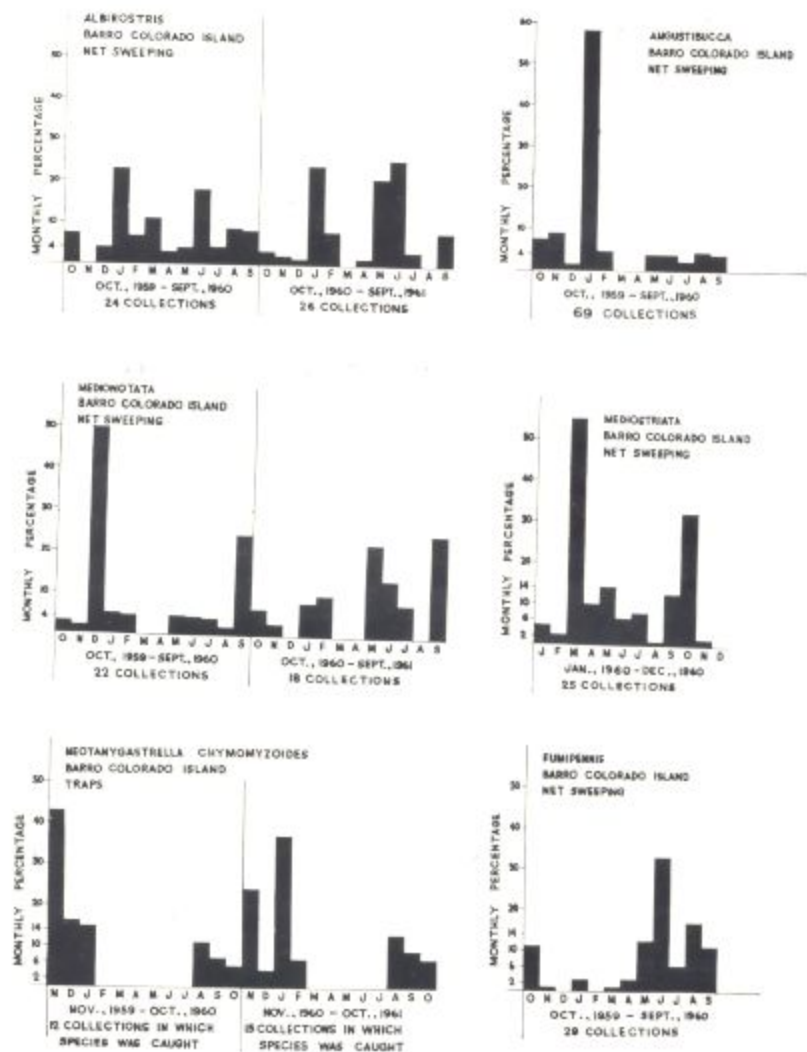

Fig. 2.—Seasonal fluctuations of drosophilid species showing population expansion during one or more months of the wet season.

the fruiting season generally extending into the wet season, through June. A second fruiting season occurs during September and October for some trees, and some plants are fruiting in every month of the year. Some trees bear fruit only once every 2 or 3 years (Allen, 1956;
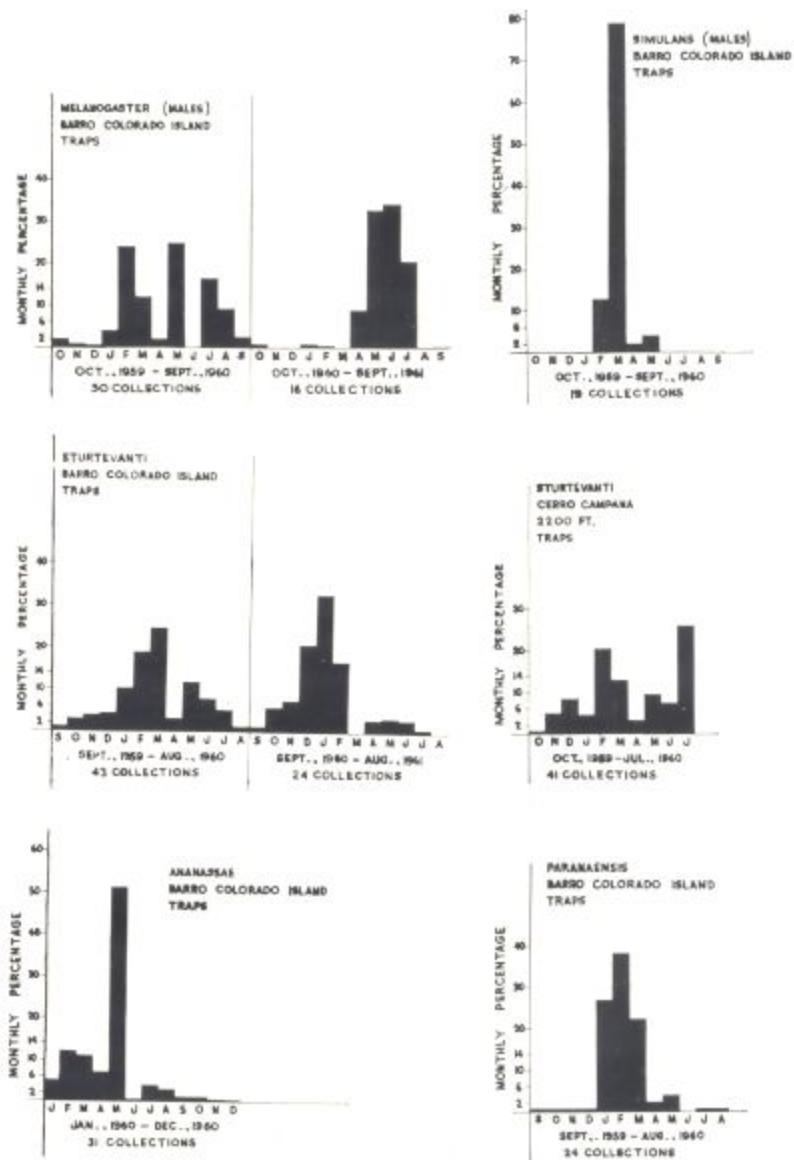

Fig. 3.—Seasonal fluctuations of *Drosophila* species showing population expansion during one or more months of the dry season.

personal observation). Trees on well drained soils in the humid tropics do not grow in pure stands as in temperate climates, but individuals of a given species are scattered throughout the forest (Allen, 1956; Rensch, 1960; Fischer, 1960).

Netted class A ground-feeders in Fig. 2 may undergo a single pronounced expansion, e.g., *D. angustibucca* during January at Barro Colorado Island; or two expansions, e.g., *D. albirostris* during January and June in two successive years at the same station. *D. medionotata* exhibited expansion during December and September the first year and during May and September the second year, with the species not found in March or April of either collection year. In these examples, the expansion period occurred either just at the end of the rainy season or during a rainy month, but *D. mediostriata* (Fig. 2) expanded its population during both a dry month (March) and a wet month (October). Two annual expansions occurring about six months apart are probably related to fruiting twice a year of certain trees, such as the *Clusia* sp., with rather dry fruits.

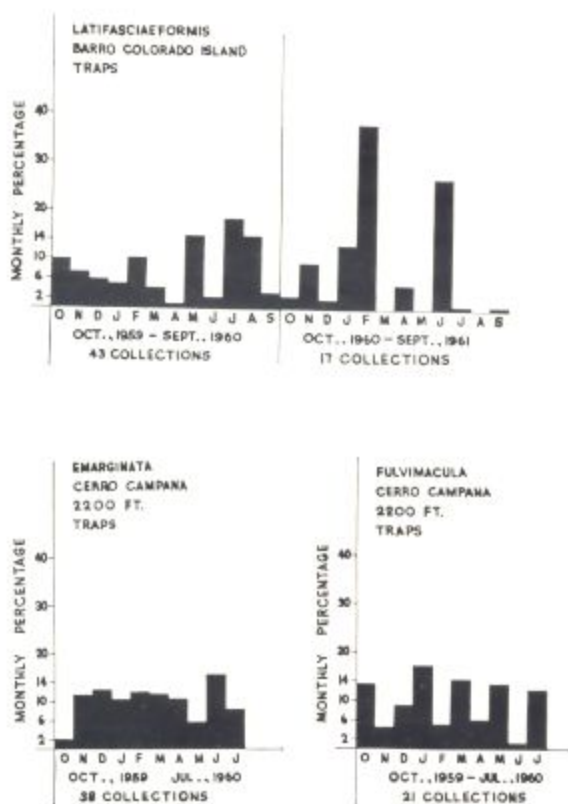*Neotanygastrella chymomyzoides* differs markedly from the *Droso-*

Fig. 4.—Little or irregular population fluctuations of *Drosophila* species.

phila species of class C not only by undergoing expansion during the wet month of November in both collection years and an additional expansion in January of the second year (Fig. 2), but the species was rarely found from March through July of either year.

Both native and cosmopolitan class C species had a population expansion during a spring fruiting month (Fig. 3). For example, the cosmopolitans, *D. simulans* and *D. ananassae*, at Barro Colorado Island showed high peaks of population in March (a dry month) and May (a wet month), respectively.

The expansion pattern of *D. melanogaster* was irregular for the two years studied. During the first year there were three separate expansions in the period from February through July. During the second year, one expansion lasted from May through July. From September through December in both years the species was found only in low numbers. *D. melanogaster* proved superior to *D. simulans* in the tropical forest just as Barker (1963) found for mixed laboratory populations of these siblings at 25 C. That *D. melanogaster* is by no means always superior was shown by Patterson (1943) for Austin, Texas, and by Pipkin (1952) for various areas in the Lebanon Mountains.

Figure 3 shows that the indigenous species *D. paranaensis* displayed a single pronounced expansion extending from January through March. The remainder of the year this species was present in fewer than 4% of the collections. Although *D. sturtevanti* occurred in fairly large numbers throughout the year, it exhibited a marked peak of population in February and March at both stations during the first year. During the second year at Barro Colorado Island, its peak extended from December through February.

Figure 4 shows that *D. emarginata* at Cerro Campana maintained almost uniform numbers. *D. latifasciaeformis* at Barro Colorado Island showed no regular pattern of fluctuation. Periods of expansion alternated with periods of low frequency in two successive years. Lack of a regular pattern is not surprising since this species has recently extended its range (Wheeler, 1957) and is probably newly subject to selection in this area.

The present work has shown that for many neotropical *Drosophila* there are definite seasonal fluctuations of population size. This agrees with the work of Bennett (1963) who described "ecologically significant seasonal changes" on Barro Colorado Island, Canal Zone. Earlier, Dobzhansky and Pavan (1950) considered seasonal fluctuations of neotropical *Drosophila* a moot question. However, Pipkin (1953) found that two trap-attractable species of the Caroline Islands fluctuated seasonally with the fruiting of a particlar tree, and Heed (1957) reported "noticeable seasonal changes in *Drosophila* population size" in San Salvador.

Seasonal fluctuations of *Drosophila* in a tropical forest, where there are no marked temperature changes, appear to be causally related to the kinds of fruits available for feeding and breeding. Class A

species, with wet season expansions, breed in many kinds of small drier fallen fruits and blossoms and also in living flowers. The fallen fruits and blossoms are particularly vulnerable to desiccation and therefore serve effectively only in the wet season. Breeding in living flowers allows class A members to survive the dry season, but populations are barely maintained when a species is confined to this breeding source. Class B and C species are able to use not only the class A breeding sources but also the advantageous fleshy fruits which fall chiefly in the dry spring months. Thus population expansions of most class B and C species occur in the spring. The regular fluctuation of *D. fulvimacula*, a fleshy fruit breeder, seems to reflect successive generations, since there are expansions and regressions of this species in alternate months. The reason for absence of seasonal fluctuations in the common species *D. emarginata* at Cerro Campana is unknown.

DISCUSSION

The wealth of *Drosophila* species in forests of central Panama is in keeping with the great species diversity of other tropical fauna discussed by Allee and Schmidt (1951). This abundance has been attributed to the constant favorable temperature, with its effect on plant life, creating an intricate array of habitats (Dobzhansky, 1950; Allee and Schmidt, 1951). As a further explanation of the complicated tropical fauna and flora, Fischer (1960) emphasizes the longer time during which evolution has operated in tropical forests in contrast to the relatively short time in temperate areas that have suffered glaciation. MacArthur and MacArthur (1961) consider the problem of tropical species diversity still not completely explained.

The chief component of the class A ground-feeding Drosophilidae of the present study is the *Drosophila* tripunctata group. This group must be very ancient if differentiation and extent of range of its members are in proportion to length of evolutionary development. Pipkin and Heed (1964) listed 54 species in the group; enough is known of adult feeding and larval breeding habits to include 27 species among class A ground feeders. The group was divided into four subgroups by Frota-Pessoa (1954), and five sets of sibling species within it have been identified by Pipkin and Heed (1964). At least five common members, *D. mediostriata*, *D. albirostris*, *D. medionotata*, *D. mediocris*, and *D. mediopicta* range from São Paulo, Brazil to Costa Rica.

Feeding and breeding primarily in fallen blossoms and small fruits accounts for the restriction of members of the large class A groundfeeding Drosophilidae to the lowland humid neotropical forest. Those species capable of expanding their populations must do so during the wet season to avoid desiccation of these feeding and breeding sources. Although numerous, the fallen blossoms and small drier fruits are inefficient for larval development; this in part accounts for the limited ability of class A members to expand their populations. Class B and C species, using fleshy fruits in addition to the former food sources, exhibit dry season expansions wherein there is a definite seasonal

pattern. Though offering efficient vehicles for larval development, fewer fleshy fruits are available because they are eaten in large numbers by forest animals. Four of the five cosmopolitan species in central Panama, *D. melanogaster, D. simulans, D. ananassae,* and *D. repleta,* belong to class C, as would be expected, since they are adapted for breeding in a dry climate.

Allee and Schmidt (1951) concluded that in the tropics small numbers of individuals generally contrast with large numbers of species in a given habitat. The present study shows variation in populations of *Drosophila* roughly dependent on the nature of fruits used for larval development, with certain exceptions. Thus in minimal populations, 24 class A species showed a relatively uniform small sample size ranging from a mean of 1.86 ± 0.89 to 4.39 ± 0.45 flies per collection. The uniformity of these minimal sample sizes of class A species depends partly on the drying out of their common feeding and breeding sources. The sizes of class B and C expanded population samples were distinctly greater than those of class A, because of the ability of the former to breed in fleshy fruits as well as in the small drier fruits. This phenomenon may represent an adaptation for survival in the dry season, which is unfavorable for the growth of microflora.

Fleshy fruit breeders do not always expand their populations, as *D. prosaltans, D. fasciola, D. repleta,* and *D. eohydei* demonstrate. Other mechanisms limit population size in these cases, perhaps genetic characteristics such as the rate of egg laying, which Stone *et al.* (1954) showed for *D. novamexicana* to be only half that of *D. hydei.* The former maintains small populations; the latter is subject to large expansions.

The present investigation has shown that large aggregations of neotropical *Drosophila* species regularly share the same adult feeding and larval breeding sources, wherein they usually undergo synchronous or closely overlapping development. These aggregations include many species belonging to the same species group, and even members of the same sibling sets. The breeding and feeding habits of members of the tripunctata group show coexistence of closely related species on an even larger scale than has hitherto been described for leafhoppers (Ross, 1957) and others. In spite of the similar breeding and feeding habits of these closely related species, each has characteristic seasonal fluctuations. A study of the microflora of the feeding and breeding sources may help explain these specific differences.

Both Andrewartha and Birch (1954) and Mayr (1963) agree that rarely are food resources of a given species fully exploited and that this failure is more characteristic of tropical than of temperate regions. Nevertheless, the fact that seasonal fluctuations occur for class A species suggests that the food supply can be so reduced by desiccation that these flies cannot be collected in certain dry months.

Park (1948) in experimental mixed populations of *Tribolium confusum* and *Tribolium castaneum* found that the species numer-

ically dominant at the beginning of the experiment eventually was the only species surviving. In nature, the near uniformity of population size of tripunctata group members allows coexistence of these closely related species. Similar sample size of these and other class A members depends largely on the detrimental effect of desiccation on their common feeding and breeding sources during the dry season. However, within the saltans group, *D. prosaltans*, with small populations, was once observed undergoing synchronous development with its close relative, *D. sturtevanti*, a species of characteristically large populations, in fruit of *Annona muricata*. Perhaps this large fleshy fruit afforded more than enough food for larvae of both species and others sharing it.

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