

LOCAL AND SEASONAL VARIATIONS IN RELATIVE FREQUENCIES OF SPECIES OF *DROSOPHILA* IN BRAZIL

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(With 1 Figure in the Text)

1. INTRODUCTION

Drosophila is a genus of flies which contains some five to six hundred described species and doubtless many as yet undescribed ones. The natural food of *Drosophila* is seldom known with precision; for example, larvae of *D. pseudoobscura* Frolowa,† one of the species most used in population studies, have never been found under strictly natural conditions. It is, nevertheless, possible to state in a general way that both adult flies and larvae feed on yeasts and bacteria which occur in fermenting substances rich in carbohydrates, such as fruits, fungi, tree sap and, in the tropics, fleshy flowers. In accordance with this, the usual technique of collecting *Drosophila* consists in attracting them to bait of fermenting banana or other fruits, or in looking for them on natural bait of the kinds mentioned above.

Different species of *Drosophila* differ in food preferences. Some fungus-feeding species seldom or never come to fermenting fruit, and vice versa. It will be shown in this article that different kinds of fruit are attractive to different species. However, except for the fungus feeders, the food specialization is not rigid, and the same fruit or other food source is usually exploited by several species. For this reason, sympatric species of *Drosophila* may be regarded as a community which depends upon a common source of food substances, for which the different species compete with each other. The competition is more keen among species which have many common food preferences than between species which live on different foods and seldom come in contact with each other. The intensity of competition depends also upon the variety of ecological niches present in the environment: if numerous ecological niches are available, in some of them a species is likely to meet fewer competitors than in others, or may even become a monopolist.

The number of species of *Drosophila* is, in general, greater in the tropics, less in the temperate, and

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† Species authorities are given in Tables 4 or 6 or where first mentioned (if in text only).

least in the cold zones; it is greater in humid and forested than in dry, steppe, or desert regions. Brazil has a rich fauna of *Drosophila*, and the variety of ecological niches open to *Drosophilae* in Brazilian forests is very large owing to the presence of many species of fruit-bearing trees and other food sources. *Drosophila* communities, in Brazilian forests, are ecological systems of great complexity. Such systems may have interesting properties not present in simpler systems found in temperate climates.

The present article reports the results of a survey of *Drosophila* populations in Brazil made chiefly during the school year, 1948-9. This survey is obviously an exploratory one, although we had the opportunity of making a cursory examination of *Drosophila* populations in the principal bioclimatic provinces of Brazil, including some rather remote and inaccessible regions.

2. MICROGEOGRAPHIC VARIATIONS

Dobzhansky (1939) noted that in Mexico and in Guatemala different assortments of species of *Drosophila* may often be found within 100-200 ft. of each other. Timoféeff-Ressovsky & Timoféeff-Ressovsky (1940) were, however, the first to submit this phenomenon to systematic study. They built, in the vicinity of Berlin, experimental fields consisting of *Drosophila* bait (nature not stated) arranged checkerboard fashion at 10 m. intervals (fields 70 × 90 and 110 × 110 m. were used). Recording of numbers of flies of different species that came to bait at different points disclosed that within these experimental fields the flies were not distributed at random, but formed nuclei of high concentration separated by relatively sparsely populated areas. These non-uniformities were more strongly pronounced in some species (*D. melanogaster* Meigen, *D. funebris* Fabricius) than in others (species of the *D. obscura* group). Dobzhansky & Epling (1944) and Dobzhansky & Wright (1943, 1947) observed in mountain forests of California that *D. pseudoobscura* forms nuclei of high concentration in the vicinity of old or diseased oak and pine trees. These non-uniformities are less striking than those found by Timoféeff-Ressovsky & Timoféeff-Ressovsky in *D. melanogaster* and *D. funebris*, and

are comparable with those in the species of the *D. obscura* group. The different degrees of non-uniformity may, in part, reflect the greater mobility of *D. pseudoobscura* as compared to *D. melanogaster* and *D. funebris*. Dobzhansky & Epling found that, under summer conditions on Mount San Jacinto, California, *D. pseudoobscura* is attracted to fermenting banana bait from distances within a 40–60 m. radius from the location of the bait. One may infer that these distances are smaller in *D. melanogaster* and *D. funebris*.

Chiefly for the purpose of their study of dispersal rates in *D. willistoni* Sturtevant, some cross-shaped experimental fields were built by Burla, da Cunha, Cavalcanti, Dobzhansky & Pavan (1950) at the Horto Florestal, near São Paulo. Each field consisted of 41 baited points spaced at 10 m. intervals and arranged in two lines 200 m. long intersecting in the middle at approximately right angles. At each baited point, about 1 kg. of fermenting banana was placed on the ground or on the fallen leaf cover. From time to time, at about 1 or 2 hr. intervals on the day of collecting, the flies that came to the bait were caught by sweeping with a cone-shaped collecting net in the air above the bait. Equal numbers of collections were made at all baits on the field, and, since several collectors participated in the work, every part of the field was taken care of by all collectors in rotation. This mitigated the disturbing influence of individual modes of collecting and made the numbers of flies caught on each bait reflect the density of the fly population in the vicinity of the baited point.

Collections were made on the same experimental field, i.e. with bait placed at the same 41 points, on 3 days, namely, on 29 December 1948, on 5 February and 11 June 1949. The total numbers of *Drosophila* flies caught on the field as a whole on these 3 days were respectively 1657, 1631, and 1452, and they belonged to at least 15, 12 and 14 different species. Among, these, species of the *willistoni* group (under this name are combined representatives of two sibling species, *D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky & Pavan, that are difficult to distinguish morphologically) (see Burla *et al.* 1950), of the *medio*-group (comprising the species *D. mediotriata* Duda, *D. mediosignata* Dobzhansky & Pavan, and *D. mediopunctata* Dobzhansky & Pavan), and *D. capricorni* Dobzhansky & Pavan were common on all 3 collecting days. *D. guaranumu* Dobzhansky & Pavan and *D. griseolineata* Duda were common in December and February (145–162 individuals in each collection) but were rare in June (1–19 individuals). *D. polymorpha* Dobzhansky & Pavan was common in February (224), but rare in December (12) and June (7), and *D. bandeirantorum* Dobzhansky & Pavan was common in June (93), but not found at all in December and February.

The distribution on the experimental field of the *willistoni* and *medio*-groups, and of *D. griseolineata* Duda and *D. capricorni* Dobzhansky & Pavan is represented diagrammatically in Fig. 1. The diagrams are constructed as follows: the number of flies of a given species found on each of the 41 baits is expressed in percentage of the total number of the same species found on the whole field on the same day. The percentages are then symbolized by black columns of different heights which rest on a cross-shaped base representing the cross-shaped experimental field with its 41 baited points. Tall black columns signify, then, that a considerable proportion of individuals of a certain species were found at certain points on the field, and low columns signify that the species was rare on some of the baits. Each arm of the cross represents the distance of 100 m. between the centre of the experimental field and one of its four ends; eleven baited points are located on each arm. The numerical data for 29 December and 11 June are published in Burla *et al.* (1950).

The diagrams show that: (1) the distribution of the flies on the experimental field is far from uniform, nuclei of high and low density being formed; (2) the location of the nuclei of high density of one species may correspond to low density of other species; and (3) the distribution of the high and low densities on the field is not permanent but shifts from month to month. For example on 7 December, species of the *willistoni* group were frequent at the end of one of the arms of the cross-shaped field (the arm directed downward in Fig. 1); 100 individuals were caught on two baits, while only 25 individuals came to the seven baits on the opposite end of the field (the arm directed upward); 368 flies were caught on the whole field. On the same day, species of the *medio*-group showed high concentration at the centre of the field and along a different arm (directed to the left in Fig. 1). *D. griseolineata* was concentrated almost entirely in the central part of the field, while the baited points toward the ends of the arms attracted few or no individuals of the species.

By February 5th, the situation had changed radically. *D. willistoni* now showed high density in the central part of the field, while the arm which contained an aggregation of this species about 5 weeks earlier showed a rather low density. Species of the *medio*-group became relatively much less common than they had been in December and somewhat more uniformly distributed. *D. griseolineata* still showed high density in the central portion of the field, but now 44 out of a total of 145 individuals of this species were found at a single baited point (no. 13) which in December was not particularly well attended (4 out of 162 individuals). By June the situation altered again. *D. willistoni*, now less frequent relative to the *medio*-group, showed an aggregation along the arm



Fig. 1.

of the cross directed to the right in Fig. 1. The species of the *medio*- group had a low density along the arm of the cross where they showed very high densities in December (directed downward in Fig. 1), but otherwise were distributed rather uniformly. *D. griseolineata* virtually disappeared—a single fly of this species was found on the field.

The data summarized in Fig. 1 are representative of a much larger body of data secured while collecting *Drosophilae* in various parts of Brazil by attracting them to banana bait. Over and over again it was observed that bait placed at points a dozen or so metres apart gives different assortments of species, the differences being unquestionably statistically significant. It was also noted that some species are more prone to form such local aggregations than others. Fig. 1 shows that *D. griseolineata* is concentrated at some baited points and wholly absent at others. *D. guarumunu* behaves similarly. *D. willistoni* and *medio*-groups tend to have more or less similar frequencies at neighbouring baited points (10 m. apart), but show non-uniformities at distances of the order of 20–40 m. *D. capricorni* was distributed relatively more evenly, although significant heterogeneities were present within 50–100 m. The degree of heterogeneity in *D. capricorni* is of the same order as found in the Californian *D. pseudoobscura*, while the behaviour of *D. willistoni* and *medio*-is about comparable to that of *D. melanogaster* and *D. funebris* as observed by Timoféeff-Ressovsky & Timoféeff-Ressovsky (1940) in Germany.

3. FOOD PREFERENCES

Two groups of factors must be considered in connexion with the microgeographic non-homogeneities in the spatial distribution of *Drosophila* species. The variety of species of trees is so large in tropical forests that if similar bait is placed at different points, some of the baited points are likely to be in the neighbourhood of trees in fruiting or flowering season, while others will be in places where natural food of *Drosophila* is scarce. More flies will be attracted to the bait in the former than in the latter places, and if different species of *Drosophila* have preferences for fruits, flowers, or sap of different trees, the relative frequencies of these species will vary from point to point. Furthermore, the flies may be sensitive to micro-environmental differences, such as more abundant moisture in depressions and relative dryness on slopes, or more light versus deeper shade depending upon the density of the vegetation. One might also suppose that representatives of each species of *Drosophila* could have an inherent tendency to aggregate in bands of conspecific individuals, but the experiments on release and recapture of marked flies in natural habitats indicate that no such tendency

exists (Dobzhansky & Wright, 1943, 1947; Burla *et al.* 1950).

We have obtained evidence of food preferences in different species by making collections not on uniform, artificial bait but on natural bait of various kinds. From data of this type we are selecting three examples which illustrate the situation as it appeared in different parts of Brazil. On 6 April 1949, collecting was made at Baguassu, near Pirassununga, in the interior of the state of São Paulo. Samples were taken on fallen fruit of the macauba palm (*Acrocomia sclerocarpa*), and, about 40 m. away, on fallen flowers of a large *Bombax* tree; about a kilometre away, near a river, another sample was taken on fallen flowers of the same species of *Bombax*, and on artificial banana bait placed in the same neighbourhood. The results of the collecting are shown in Table 1. Macauba and banana fruits were clearly more attractive than *Bombax* flowers to *D. willistoni*, while *D. guarumunu* and species of the *medio*- group preferred the flowers. *D. campestris* (a new species of the *cardini* group) and *D. caponei* Pavan & Da Cunha occurred almost entirely on the flowers and ignored the fruits in the neighbourhood away from the river but were rare on the same species of flowers in the river neighbourhood. *D. willistoni* ignored *Bombax* almost entirely in the first, but not in the second, neighbourhood.

Table 1. Percentages of various species of *Drosophila* in samples collected in two neighbourhoods near Pirassununga, São Paulo

Species or group	Neighbourhood I		Neighbourhood II	
	Macauba fruits	<i>Bombax</i> flowers	<i>Bombax</i> flowers	Banana bait
<i>willistoni</i>	63.8	0.6	16.9	31.9
<i>guarumunu</i>	3.2	46.1	51.8	40.8
<i>medio</i> - group	11.7	22.6	20.3	11.5
<i>campestris</i>	0.9	22.9	1.7	0.9
<i>polymorpha</i>	7.1	0.5	7.6	11.9
<i>calloptera</i> group	7.1	—	—	0.3
<i>bandeirantorum</i>	0.1	—	1.2	2.0
<i>caponei</i>	—	5.7	—	—
Other species	6.1	1.6	0.4	0.7
Individuals collected	889	646	815	652

On 28–31 March 1949, collections were made on fallen fruits of various forest trees, and on artificial bait prepared from fermenting goiaba (*Psidium guayava*) fruit, in the vicinity of Park headquarters, Iguassú National Park, Paraná. Only common names of the trees were given by an experienced forest ranger; some of their scientific equivalents are, according to Dr George Black of the Instituto Agronomico do Norte, probably as follows: jaracatia = *Jacaratia* sp.; coquinho = a species of palm; canela amarela = *Nectandra grandiflora*; alecrim = *Marctia* sp. (?);

Table 2. Percentages of various species of *Drosophila* collected on different fruits at Iguassú National Park, Paraná

Species or group	Jaracatia	Coquinho	Canela amarela	Aguahi	Alecrim	Cauna	Pitanga	Goiaba
<i>willistoni</i>	68.0	87.2	—	48.5	40.2	31.9	77.9	62.7
<i>nebulosa</i>	0.3	0.3	0.9	14.9	17.1	28.1	3.9	0.6
medio- group	20.3	1.6	16.4	11.1	4.9	5.0	3.9	1.8
<i>guaramumu</i>	3.0	5.0	81.9	17.2	23.5	32.6	14.3	6.4
<i>polymorpha</i>	8.3	6.0	0.9	8.4	14.3	2.1	—	28.3
Others	—	—	—	—	—	0.2	—	0.1
Individuals collected	300	367	116	586	286	427	154	3088

Table 3. Percentages of various species of *Drosophila* collected on different fruits at the Instituto Agronomico do Norte, Belem do Pará

Species or group	Terra Firme		Igapó						
	Banana bait	Bread-fruit	Banana bait	Bacaba	Murumurú	<i>Clusia</i> sp.	<i>Hura</i>	<i>Matisia</i>	<i>Lucuma</i>
<i>willistoni</i> group	79.2	64.0	58.1	15.0	40.9	56.7	12.6	92.3	75.9
<i>fumipennis</i>	11.1	—	2.0	—	—	20.0	1.0	—	11.8
<i>nebulosa</i>	0.3	—	3.0	—	0.7	—	0.5	—	—
<i>simulans</i>	—	—	0.1	—	4.7	—	—	—	—
<i>sturtevanti</i>	1.1	—	15.2	—	0.3	—	—	—	—
medio- group I	0.3	13.5	0.7	55.0	—	—	81.6	—	—
medio- group II	0.3	9.6	0.8	—	—	—	0.5	—	5.6
<i>camargoi</i>	6.7	6.1	6.6	5.0	—	—	—	6.7	—
<i>fumosa</i>	—	3.8	0.6	—	—	—	—	—	—
<i>peruviana</i> (?)	—	—	0.1	—	51.1	—	—	—	—
<i>repleta</i> group	—	0.4	6.0	—	1.8	—	—	0.4	0.3
<i>canalineá</i>	0.6	—	4.1	10.0	0.3	—	0.5	—	0.6
<i>calloptera</i> group	0.1	—	0.1	—	—	—	—	—	2.9
Others	1.7	2.6	2.7	15.0	—	23.4	3.2	0.7	2.3
Number of flies	360	261	712	40	276	30	191	284	341

cauna = *Ilex* sp. (?); pitanga = *Eugenia* sp. The data are summarized in Table 2. The commonest species in the region is *D. willistoni*, but it was conspicuously absent on canela amarela fruit. In another part of the forest, where a canela amarela tree stood near an alecrim tree, some *D. willistoni* were, however, present on the fruit of the former, thus showing that they are not completely unacceptable to this species. *D. nebulosa* preferred aguahi, alecrim and cauna fruits, while *D. polymorpha* chose the goiaba bait and alecrim fruit. Canela amarela was most acceptable to *D. guaramumu* and to a species of the medio- group.

Drosophila population samples were taken at various points in lowland ('igapó') and on higher ground ('terra firme') forests within 1-3 km. from the Instituto Agronomico do Norte, Belem do Pará, on 5-8 May 1949. Apart from artificial banana bait, we collected on fallen fruit of the breadfruit tree (*Artocarpus incisa*), bacaba palm (*Oenocarpus distichus*), murumurú palm (*Astrocaryum murumuru*), *Clusia* sp., *Hura crepitans*, *Matisia caudata* and *Lucuma* sp. We are greatly obliged to Dr George Black for naming

these fruits. As many as 34 easily distinguishable species and species groups of *Drosophila* were found, several of them undescribed. An extract from the data is presented in Table 3. Species of the *willistoni* group (*willistoni* Sturtevant, *paulistorum* Dobzhansky & Pavan, *equinoxialis* Dobzhansky, and *tropicalis* Burla & da Cunha) were encountered in all samples, and in most cases constituted more than a half of all *Drosophila* found. Fruits of *Hura crepitans*, of the bacaba palm, and of the breadfruit tree attracted an apparently undescribed species of the medio- group, which was rare or absent on other fruits. A species tentatively identified as *D. peruviana* Duda was common on the fruits of murumurú palm, although in June 1948, this species was found abundantly also on banana bait exposed in the same locality. *D. fumipennis* was fairly abundant on fruits of *Lucuma* and *Clusia*, and on banana bait, but rare on other fruits.

The food preferences exhibited by *Drosophila* species are, thus, not rigid. It is clear that different fruits attract different assortments of species of *Drosophila* in the same neighbourhood. But it is also

true that the same fruit may be visited by a given species in some but not in other neighbourhoods. Just what causes these variations in the attractiveness of the same kind of fruit is conjectural. Wagner (1944) has shown that the two closely related species, *D. mulleri* and *D. aldrichi*, have different nutritional requirements, so that strains of yeasts which satisfy one of these species may or may not be acceptable to the other. It is possible, then, that differences in the microfloras living on the same species of fruit in different neighbourhoods may be responsible for the different sets of *Drosophila* species which are attracted. The microclimatic conditions in which the fruits are placed are obviously another possible source of the variations. However that may be, it appears that most fruit-feeding species of *Drosophila* can, if necessary, subsist on many different kinds of fruit. Their ability to develop on standard laboratory culture media attests their rather omnivorous habits. Nevertheless, if choice is available, different *Drosophilae* do select different fruits, and some species are more and others less discriminating in their choices. The fungus-feeders are, of course, a different story: most of them do not come, or come rarely, to baits of fermenting fruits. We made no effort to collect the numerous fungus-feeding species, except when we saw them on fungi which abound in the humid interior of tropical rain forests. These collections are not included in the materials reported in this article.

4. SEASONAL CHANGES

Drosophila populations of temperate and cold lands are profoundly affected by radical changes in the natural environments produced by alternation of the seasons. By far the best data on seasonal changes in *Drosophila* populations are those of Patterson (1943) for the vicinity of Austin, Texas. Both absolute and relative abundance of species of *Drosophila* undergo cyclic changes with less striking variations from year to year. Some species have a sharp seasonal maximum and virtually disappear during some months; other species show 2- or even 3-yearly maxima, and can be collected at any time. The relative frequencies of different species change from month to month.

Contrary to the rather widespread misapprehension, seasonal changes are by no means lacking in the tropics. In most of Brazil, striking changes in the natural environment are caused by alternation of wet and dry seasons. In coastal rain forests and in parts of the Amazon basin, temperature and humidity are high enough throughout the year so that the inhabitants do not suffer from cold or desiccation. Nevertheless, different species of plants have different flowering and fruiting seasons and, accordingly, the environment is in a constant flux also for animals, whether fruit-feeding or not. Fixity of flowering and

fruiting seasons occurs even in climates which are, from a purely meteorological standpoint, among the most constant on earth, e.g. the climate of the Espirito Santo Island, in the New Hebrides (Baker, 1947).

During 1948 and 1949, repeated collections of *Drosophila* were made at three collecting localities in the state of São Paulo, namely, at Vila Atlântica in the coastal rain forest, at Mogi das Cruzes on the plateau, and at Pirassununga in the interior. Care was taken to have the bait placed always at the same points, so that any differences in the relative frequencies of *Drosophila* species could not be ascribed to local variations in food distribution. The material collected was classified as a rule in the field with the aid of a binocular microscope. A summary of the data is presented in Table 4. The same table shows also the results of two collections made at Monjolinho, in the central part of the state of Goyaz, at the beginning of the rainy and of the dry seasons respectively. Also included are collections on banana bait made near the canal ('igarapé') Murutucú, on the grounds of the Instituto Agronomico do Norte, Belém, state of Pará, and, finally, the collections at Mogi das Cruzes made in 1946 and 1947. The latter collections were not necessarily made at the same points as the 1948-9 collections, although they were made certainly within the same neighbourhood. Seasonal changes near São Paulo (at Cantareira) have been discussed on pp. 2-4.

Table 4 shows that the relative frequencies of species of *Drosophila* in tropical climates undergo striking changes from month to month. Vila Atlântica, although located south of the Tropic of Capricorn, has a superhumid tropical climate. At Santos, some 20 km. to the east, the rainfall is above 100 mm. per month during the driest season (July and August), and between 200 and 300 mm. per month during the wettest season (January to March); the temperature means range from 18.6° (July) to 25.2° C. (February). The rainfall at Vila Atlântica is, if anything, more abundant than at Santos. Species of the *willistoni* group (*D. willistoni* and *D. paulistorum*) constituted about 77% of the total *Drosophila* catch in January, but they were both absolutely and relatively less common (5-10%) in August and September. Conversely, *D. capricorni* and species of the *medio-* group were common from August to November, and again in May and July, but rare in January and March. January and March saw an upsurge of the population of *D. fumipennis*, while September showed the highest observed frequencies of *D. sturtevantii* and *D. griseolineata*.

Mogi das Cruzes lies at about 850 m. above sea level, some 50 km. from the city of São Paulo. The monthly temperature means vary from 15° (June-August) to 21-22° C. (January-March), and precipitation varies from 30 mm. (July) to 208 mm. (January). As at Vila Atlântica, the species of the *willistoni* group

Table 4. Seasonal changes in frequencies of species of *Drosophila*

Locality and date	<i>willistoni</i> group	<i>capricorni</i> Dobzhansky & Pavan	<i>funiberris</i> Duda	<i>boettcheri</i> Pavan & da Cunha	<i>nebulosa</i> Sturtevant	<i>simulans</i> group	<i>sturtevanti</i> Duda	<i>polynorpha</i> Dobzhansky & Pavan	<i>cardinoides</i> Dobzhansky & Pavan	<i>campestris</i> Pavan	<i>medio</i> -group	<i>bandeiratorem</i> Dobzhansky & Pavan	<i>timmyans</i> Sturtevant	<i>palldipennis</i> Dobzhansky & Pavan	<i>griseolineata</i> Duda	<i>guarant</i> group	<i>guarantum</i> Dobzhansky & Pavan	<i>funosa</i> Pavan & da Cunha	<i>canthina</i> Patterson & Mainland	<i>nitescens</i> Patterson & Mainland	<i>repleta</i> groups	<i>mitis</i> Dobzhansky & Pavan	Others	Nos. of species	Nos. of individuals	
Vila Atlantica:																										
21-22. viii. 48	10.2	34.4	7.5	0.5	0.6	0.6, 0.5, 0.3	0.0, 0.0, 0.0	1.1	0		<i>cardinoides</i> Dobzhansky & Pavan		0.2		0.8	0.3	0.3	0.3			1.3		3.4	22	1100	
20. ix. 48	5.0	10.1	10.0	0.03	0.6	0.5, 0.4, 0.3	0.2	1.1	0		19.3		0.2		9.3	0.3	0.9	0.9			0.5		2.0	19	3700	
24. x. 48	13.0	30.0	21.6		0.2	10.2	1.1	1.3			0.4				0.05	0.03	0.1	0.1			0.5		1.4	13	440	
16. iii. 49	77.3	0.3	18.1		0.01	1.3	1.0	1.3			0.4	0.03			0.05	0.03	0.1	0.1			0.6		0.1	14	614	
10. iii. 49	30.0	1.6	52.8		0.05	6.1	2.6	1.2	1.2		2.7	0.06			0.06	0.2	0.05	0.4	0.4		0.06		3.6	20	152	
27. iv. 49	16.8	15.5	15.4		0.1	5.5	0.7				44.7				0.8	1.5	0.1	0.1	0.4		0.5		3.6	15	720	
25. viii. 49	14.7	16.5	33.3	0.1		0.1	0.2				25.3	0.3			0.7	0.1	0.1	0.6	0.6		0.5		1.7	20	1058	
1-16. ix. 46	1.3	0.5			14.6	0.3	1.0	0.9	0.9		51.1	0.6	6.4		0.5	1.8	0.4				4.6		8.1	17	769	
15-16. xi. 46	12.8	3.4		0.4	0.1	2.3		0.4	0.4		4.9	5.0	3.3		4.9	10.6	1.0			0.8	1.5	0.4	0.4	15	266	
11. v. 47	13.9			0.06	0.1	35.4	0.5	2.1	3.5	0.06	8.8	4.0	3.3	0.5	1.1	1.2	1.2			1.3	20.9	3.52	0.9	18	1732	
14-28. xii. 47	36.8			0.1	1.2	0.6	0.3	21.6	0.03		25.8	2.4	0.5		1.1	0.2	7.4		0.03		0.5	0.1	0.5	20	3330	
4. ix. 48	2.1	6.7	0.1	3.1		2.5	0.1	0.6	0.1		53.8	17.5	2.3		0.9	7.7	0.1		0.1	0.1	0.8		1.4	24	954	
Mogi das Cruzes:																										
19. ix. 48	1.8	6.0		1.0		2.3		0.3			68.2	5.0	1.6		3.4	7.4			0.2	0.2	0.7		2.1	18	1028	
24. x. 48	3.0	10.1		1.8		25.9		0.6	0.1		42.0	2.5	2.8		3.4	4.4	0.02	0.2	0.2	0.6	0.7		1.7	25	4473	
17-26. xii. 48	20.8	15.1	1.1	1.0	0.4	6.0	0.05	1.9			18.5	3.2	2.0	0.04	1.8	1.1	6.4		0.2	0.2	0.8		0.5	23	2361	
19-20. ii. 49	41.5	10.1	0.1	14.7	1.8	3.5		1.6		0.3	17.4	0.5	0.4		4.8	1.5	2.2		0.07		0.1		0.4	10	1399	
22. v. 49	3.2	2.2		8.4	0.2			1.9	0.4		68.0	1.9	0.2		0.4	5.1	0.9		0.2		0.4		1.0	17	534	
28. vi. 49	2.1	31.9		1.3				2.0			33.4	25.0	1.3		0.4	2.5	0.1		0.3		0.1	0.1	0.4	16	667	
30. viii. 49	0.9	0.9		0.6		0.2	0.1	0.9			84.2	8.4	1.3		0.1	0.5			0.1		0.1		1.2	19	888	
Prassumunga:																										
7. ix. 48	4.2	0.2	0.3	1.0	0.2	54.1	0.2	0.2	0.3		9.5	0.2	1.0		0.2	1.9	6.7	1.0	0.7	12.3	1.1		4.9	24	612	
11. x. 48	2.2	0.04		0.3	0.9	69.6	0.04	1.5			2.8	0.4	1.2		0.2	0.2	18.5	0.04	0.3	0.04	0.4		1.5	22	2324	
9. xii. 48	34.3	0.2			3.8	19.6	0.5	7.3			4.2	0.2	1.2	0.2		2.2	2.2	0.2	1.0	0.3	0.4		5.5	16	601	
10. ii. 49	46.9			0.6	4.7	2.6	0.3	21.8		0.8	7.4	1.1		0.6			11.3	0.2					0.6	16	1605	
6. iv. 49	50.1	0.5	0.3				1.0	9.0	0.2		12.0	0.9					19.0	0.2					5.0	18	1548	
14. vi. 49	25.3	0.2		2.7				7.2		0.7	28.2	1.0					32.0	0.2					2.7	9	415	
1. viii. 49	7.4	0.1		0.7	0.6	6.8		4.3			20.5	1.4	0.5			0.7	52.3				0.5	0.1	4.4	18	879	
Montolinho, Coyzaz:																										
1-2. vi. 48	3.0	1.3		5.7	63.8	4.9	0.5	4.4		2.7	2.3		0.4	0.05		0.3	3.0	0.1	0.5		3.3	0.2	3.4	24	1050	
7-to. vi. 49	21.1	3.0	4.5	0.9	5.2	6.3	7.8	0.1		0.5	21.9		0.1	0.06		1.8	11.4	0.2	0.1	0.1	8.5	1.4	4.6	28	1817	
Belem:																										
1-to. vi. 48	76.3	0.2			0.4	0.3	4.7	0.5	0.1		1.0					0.9		0.2	0.3		0.5	1.9	12.6	26	16455	
5. v. 49	58.1		2.0		3.0	0.1	15.1	0.3	0.6		1.5					0.1		0.9	4.1		4.8	0.1	10.0	36	1718	
17-28. vii. 49	54.2		0.9		0.1		7.9	7.9	0.1		5.6					0.2		0.9	0.1		3.5	15.7	3.8	22	1978	
9-to. ix. 49	52.4				0.6		15.7	3.2	0.4		6.5					1.0			0.2		5.5	12.7	1.0	21	1692	

showed highest frequencies during the warm and humid season (December–February), and underwent an eclipse during the cool and dry season (May–October). The *medio-* group of species showed the converse change, having been predominant (68%) in September and May, and less frequent (17–19%) in December and February. In contrast to Vila Atlantica, *D. capricorni* maintained rather high frequencies during the warm season (October–February), became rare in May, and turned out to be the commonest species in late June. *D. griseolineata* reached maximum expansion of its population at Mogi later (December) than at Vila Atlantica (September), and *D. fumipennis* and *D. sturtevanti* remained rare throughout. Instead, there occurred at Mogi brief outbursts of high frequencies of *D. bocainensis* (February), *D. simulans* Sturtevant (October), and *D. bandeirantorum* (September and June).

Pirassununga has dry (precipitation 21, 14 and 28 mm. in June, July and August respectively) but fairly warm winters (18.4–19.6° C.), and humid and warm summers (188 mm. precipitation and 23.5° mean temperature in January). The desiccation during the dry season is doubtless a limiting factor in the reproduction of *Drosophila* populations. As in the preceding two localities, the *D. willistoni* group (more than 90% of individuals being *D. willistoni* and *D. paulistorum* less than 10%) showed high frequencies during the wet and hot season and low ones during September and October. *D. simulans* showed a striking change from the status of the dominant species in September and October to an ostensible disappearance from April to June. The *medio-* group was fairly frequent from April to August and less so at other times. *D. guaramumu* was common at all times, and became predominant in June. *D. polymorpha*, *D. nigricurvia* and *D. nebulosa* have each shown brief spurts of population growth.

The plateau of central Goyaz has fairly even temperature (monthly means from 18.3° to 22.6° C. at Santa Luzia) throughout the year, but has sharp dry seasons (10 mm. or less precipitation per month from June to August) and rainy seasons (242–321 mm. per month from November to March). Table 4 shows significant alterations of frequencies of several species between November 1948 and June 1949.

Belem lies in the superhumid equatorial zone. Here the mean temperature of the warmest month (26.8° C. in October) is 1.5° C. higher than that of the coolest (February), and the all-time high temperature record (36.6° C.) is 17.4° C. higher than the all-time low (19.2° C.). The precipitation varies from 72 mm. (November) to 402 mm. (March) per month, but the mean relative humidity changes only from 84% (October) to 94% (February). Nevertheless, our data show that the relative frequencies of *Drosophila* species are far from constant, except that the *D. willis-*

stoni group remains predominant, and within that group the species *D. paulistorum* remains more frequent than *D. willistoni*, *D. tropicalis* Burla & da Cunha and *D. equinoxialis*, apparently in that order. Significant changes in abundance have been recorded for *D. nebulosa*, *D. fumipennis*, *D. sturtevanti*, *D. polymorpha*, *D. canalinea*, *D. mirim*, *D. peruviana* and *D. camargoi*.

Seasonal pulsations of population size occur in Brazilian *Drosophilae*, and there is no evidence that the amplitude of these pulsations is correlated with seasonal constancy or variability of the climate as evaluated on the basis of purely meteorological elements. To what extent the changes in the composition of *Drosophila* populations recorded in 1948–9 reflect the cyclic changes in the environment is an open question. Observations made at Mogi das Cruzes in 1946 and 1947 are relevant at this point (Table 4). *D. willistoni* was rare in September 1946, and common in December 1947; this agrees with the behaviour of this species group in 1948–9. But *D. capricorni* constituted 15% of the total *Drosophila* population in December 1948, but was not recorded at all in December 1947. *D. simulans* was abundant in May 1947, but seemed to be absent in May 1949. *D. polymorpha* showed a high frequency in December 1947, and a low one in December 1948, while *D. griseolineata* did the opposite. Most striking of all are the high frequencies of *D. mirim* and of species of the *repleta* group recorded in May 1947; in 1948–9, these species never rose in frequency above 1% of the total.

The meaning of these variations is in doubt since, as pointed out above, the 1946–7 samples at Mogi das Cruzes were not collected at exactly the same points as the 1948–9 samples. It may, however, be pointed out that Patterson (1943) recorded variations from year to year in seasonal abundance of some *Drosophila* species in the warm temperate climate of Texas. The numbers of sympatric species of *Drosophila* in most parts of Brazil is, however, greater than in Texas. This may create so complex a system of mutual relationships between the competing species that annual recurrence of the same set of relative frequencies may become improbable. In other words, climatic year-to-year variations may influence the complex tropical communities of *Drosophila* to a greater extent than they influence the relatively simpler communities in temperate countries.

5. COMMON AND RARE SPECIES

The variations in the abundance of *Drosophila* species in different neighbourhoods, on different foods, and at different times limit the value of any conclusions that we may reach regarding the commonness and rarity of species in a bioclimatic zone or a geographic

region. Nevertheless, an ecologist or a geneticist cannot ignore the distinctions between species that occur practically wherever one makes a collection in a large region, and species which occur sporadically, only in some environments, or only at certain seasons. Species of the former kind are likely to be adaptively more versatile and able to occupy a greater variety of habitats, while species of the latter kind are more specialized and confined to fewer habitats.

We collected samples of *Drosophila* populations in seventeen 'regions' of Brazil enumerated in Table 5 (not counting small samples from two other regions). The thoroughness of the collecting in different regions varied greatly, from a single sample of 241 flies taken in a circumscribed neighbourhood in the territory of Guaporé, to 31 samples taken within

samples. They were present in all regions and in all localities in which collections were made, and were absent in only 18 samples. Among the 18 samples which failed to include *D. willistoni*, 6 samples are small (6-27 individuals), 3 come from the desert (caatinga) of Bahia, and the remainder from special environments which appear to be avoided by species of this group. These are fruits of marfim (Apocynaceae, *Couma* sp.?), and mirixí (*Byrsonima*) in the forest of Rio Branco, fruits of apixona (Myrtaceae) and patauá (*Oenocarpus bataua*), flowers of envira (Anonaceae) and shells of brazil-nut (*Bertolettia excelsa*) on the Rio Negro, jaca fruits (*Artocarpus integrifolia*) in a garden at Palmares, Acre, fruits of canela amarela (*Ocotea? Nectandra?*) at Iguassú, Paraná, and a fermentation tank for sugar-cane juice at Imperatriz,

Table 5. *Numbers of localities, samples, and individuals collected in the seventeen regions of Brazil in which Drosophila collecting has been made*

Region	Localities	Samples	Flies collected
Territory Rio Branco, savanna	5	13	2,989
Territory Rio Branco, forest	1	9	1,725
Lower Rio Negro	6	31	3,463
Western Acre (Cruzeiro do Sul)	2	4	2,084
Eastern Acre (Palmares)	1	9	1,864
Territory Guaporé (Porto Velho)	1	1	241
Marajó Island	3	4	1,668
Belem do Pará	1	15	23,832
Middle Tocantins, Maranhão	2	7	2,708
Central Goyaz	2	3	4,297
Caatinga of Bahia	2	8	4,235
São Paulo, interior (Pirassununga)	1	11	10,986
São Paulo, plateau	2	15	23,140
São Paulo, coast	2	9	16,174
Paraná, Central (Lambedor)	1	1	7,098
Paraná, Western (Iguassú)	2	15	8,422
Rio Grande do Sul (Santo Angelo)	1	1	1,503
Total	35	156	116,429

5 days on various natural foods in five localities of lower Rio Negro, and to 15 samples taken in different months and years on the plateau of São Paulo (Mogi das Cruzes and Cantareira). We distinguish, somewhat arbitrarily, between 'regions', 'localities' and 'samples'; 156 samples were taken in 35 localities in 17 regions, with an aggregate of 116,429 individuals.

Table 6 summarizes the data for different species and species groups. The figures in this table indicate the numbers of regions, localities and samples in which a given species held the first, the second, or the third, or a lower rank in relative frequency, or was not found at all.

Species of the *willistoni* group are clearly the most common and widespread in Brazil. They occupy the first place in abundance in 9, and the second or third place in 6 more of the 17 regions, and hold the first place in 13 out of 35 localities and in 67 out of 156

Maranhão. A few *D. willistoni* have, however, been found on other occasions on jaca and canela amarela fruits and on *Bertolettia* shells.

Of the four sibling species which compose the *willistoni* group, *D. willistoni* s.str. is the most widely distributed, and is the only one so far found in southern Brazil (Rio Grande do Sul and Paraná). It is the most frequent species of the group in the territories of Rio Branco, Acre, and Guaporé, as well as on Rio Negro, in Maranhão, Goyaz, Bahia, and in the interior of São Paulo. The distribution region of *D. paulistorum* is included in that of *D. willistoni*; the former is known to extend from São Paulo to the northern part of the Amazon Basin (Rio Branco). At Belem *D. paulistorum* is more common than *D. willistoni*, apparently at all seasons. On the plateau and on the coast of São Paulo, *D. willistoni* retains the first place during the cooler seasons but surrenders it to

Table 6. Numbers of regions, localities, and samples in which certain species, or species groups of *Drosophila* held the first, second or third, or other frequency ranks

Species or species group	Regions (17)				Localities (35)				Samples (156)			
	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent
<i>willistoni</i> group	9	6	2	—	13	18	4	—	67	48	23	18
<i>fumipennis</i>	—	2	6	9	3	3	11	18	12	23	23	98
<i>capricorni</i>	—	1	7	9	—	2	7	26	1	11	26	118
<i>nebulosa</i>	4	—	11	2	11	1	14	9	25	19	48	64
<i>bocainensis</i>	—	—	12	5	—	—	14	21	—	8	31	117
<i>prosaltans</i> Duda	—	1	7	9	—	2	10	23	—	5	21	130
<i>sturtevanti</i>	1	2	8	6	3	3	11	18	6	9	34	107
<i>simulans</i> group	—	4	10	3	—	6	13	16	5	18	28	105
<i>ananassae</i> Doleschall	—	—	4	13	—	—	4	31	—	2	6	148
<i>polymorpha</i>	—	2	11	4	—	2	15	18	—	16	55	85
<i>cardinoides</i>	—	2	11	4	—	2	15	18	—	9	31	116
<i>neocardini</i> Streisinger	—	—	4	13	—	—	5	30	—	—	10	146
<i>campestris</i>	—	1	10	6	—	3	18	14	—	19	38	99
<i>guarani</i> and <i>guaru</i> Dobzhansky & Pavan	—	—	11	6	—	—	16	19	2	6	36	112
<i>guaramunu</i>	2	2	3	10	2	3	4	26	9	13	25	109
<i>griseolineata</i>	—	—	5	12	—	—	6	29	—	2	20	134
<i>bandeirantorum</i>	—	—	5	12	—	—	6	29	—	3	27	126
<i>immigrans</i>	—	—	5	12	—	—	5	30	—	—	16	140
<i>medio</i> -group	1	6	9	1	3	13	13	6	27	60	37	32
<i>fumosa</i>	—	—	7	10	—	—	8	27	—	—	14	142
<i>camargoi</i> Dobzhansky & Pavan	—	—	5	12	—	—	7	28	—	5	10	141
<i>dreyfusi</i> Dobzhansky & Pavan	—	—	4	13	—	—	4	31	—	—	10	146
<i>pallidipennis</i>	—	—	5	12	—	—	5	30	—	—	13	143
<i>canalineá</i> group	—	1	9	7	—	1	11	23	—	2	31	123
<i>repleta</i> group	—	1	13	3	—	1	20	14	—	7	52	97
<i>fulvamacula</i> Paterson & Mainland	—	1	8	8	—	3	11	21	1	6	18	131
<i>annulimana</i> group	—	—	7	10	—	—	9	26	—	—	16	140
<i>mirim</i>	—	2	10	5	—	4	11	20	1	11	24	120
<i>nigricurria</i>	—	—	4	13	—	—	4	31	—	1	9	146
<i>calloptera</i> group	—	—	13	4	—	1	18	16	—	8	39	109

D. paulistorum during the warmer season. The other two species, *D. tropicalis* and *D. equinoxialis*, are known only from the basin of the Amazon, and thus their distribution regions are included in that of *D. paulistorum*. They are, as a rule, less common than either *D. willistoni* or *D. paulistorum*, except that in some samples taken in the north-eastern part of Marajó Island (Cape Maguari) *D. tropicalis* and *D. willistoni* proved to be equally common and *D. paulistorum* rare. *D. willistoni* may, thus, be regarded ecologically the most versatile of *Drosophila* species in Brazil. *D. paulistorum* is superior to it only in some superhumid and hot climates (Pará, coast of São Paulo, close second on Rio Negro), while

D. nebulosa forges ahead in savanna and caatinga environments.

D. nebulosa is the dominant species in four regions: savanna of Rio Branco, Maranhão, Goyaz, and the Bahian caatinga, in all of which it displaces *D. willistoni* to the second or the third place in frequency. It is significant that *D. nebulosa* is nowhere found to occupy the second or the third place in frequency; this species is dominant in regions which have a prolonged dry season, but in regions with a more even distribution of rainfall it rarely attains high abundance. The 11 localities and 22 out of the 25 samples in which *D. nebulosa* was the commonest species are in the four above-named regions. In 7 out of the 8

samples from the caatingas of Bahia it had frequencies in excess of 50% of the total; out of the 13 samples from the savanna of Rio Branco, *D. nebulosa* had frequencies above 50% in 8 samples, one of which had 686 flies, 683 of which were *D. nebulosa*. At Monjolinho, Goyaz, *D. nebulosa* was the most prevalent species in November 1948, but it held only the fifth place in frequency in June 1949, *D. willistoni* being the most frequent species at that time. In general, *D. willistoni* competes with *D. nebulosa* rather successfully in savanna environments, but surrenders to the latter the driest caatingas. Some of the food preferences of *D. nebulosa* are similar to those of *D. willistoni*. Thus, *D. nebulosa* was absent in the sugar-cane fermentation tank at Imperatriz, and rare on jaca fruits in Bahia, on marfim in Rio Branco, and on canela amarela at Iguassú, Paraná.

D. fumipennis is a member of the *willistoni* group in a broad sense, which includes in the Brazilian fauna, the four *willistoni*-like sibling species and also *D. capricorni*, *D. fumipennis*, *D. bocainensis* and *D. nebulosa*. *D. fumipennis* is the second most frequent species on Rio Negro and the third on the coast of São Paulo. It is also fairly common in Pará and in Acre. Its environmental preference thus seems to be for superhumid tropical climates, although it occurs occasionally even in the savannas of Rio Branco and in Goyaz. It has reached the status of dominant species in two samples from the coast of São Paulo, and in ten samples from Rio Negro. On Rio Negro it is quite abundant on some species of fruits and wholly absent on others. In May 1948, it was found in the vicinity of Belem on banana bait and on fruits of *Clusia* sp., *Hura crepitans* and *Lucuma* sp., but not on breadfruit, bacaba and murumuru palms or *Matisia* sp. (Table 3). *D. fumipennis* must be characterized as a common and ecologically fairly versatile species, but inferior in both respects to *D. willistoni* and *D. nebulosa*.

D. capricorni is a common species on the plateau and on the coast of São Paulo, where it reaches the status of the third and the fourth commonest species respectively. Elsewhere in Brazil it is rare, although a few individuals of this or a very similar species have been found even in the equatorial zone (forest of Rio Branco, Pará, Maranhão) and in Goyaz. *D. bocainensis* is a widespread but usually infrequent species.

Except for the Bahian caatingas where they seem to be absent, species of the *medio*-group are, after those of the *willistoni* group, most widespread in Brazil. They hold the first place in abundance in the plateau region of São Paulo (*willistoni* being a close second), the second place in the forest of Rio Branco, in western Acre, and on the coast of São Paulo, and the third place in eastern Acre, in Goyaz, and in Rio Grande do Sul. It must be noted, however, that this group consists of at least eight morphologically

rather similar species, at least four of them undescribed, and most or all breeding with difficulty on the standard banana agar laboratory medium. Our field notes show that, in contrast to the sibling species of the *willistoni* group, the species of the *medio*-group do not occur all together in the same samples, but are, on the contrary, ecologically well differentiated. A systematic revision of the group is needed before its ecology can be successfully studied. *D. guarumunu* has not been found at all in the nine of our regions closest to the Equator (Table 5), but it seems to be the dominant species or the second most frequent species in the southern part of Brazil: Rio Grande do Sul, central and western Paraná, and in the interior of São Paulo. It is fairly common on the plateau of São Paulo, and occurs on the coast of São Paulo and in central Goyaz. Table 1 and Table 2 show that it has food preferences of its own, different from those of *D. willistoni* and *D. nebulosa*. At Santo Angelo, Rio Grande do Sul, *D. guarumunu* was found predominant on pumpkin fields, while citrus fruits attracted relatively few of them. The nuclei of high population density of this species at Cantareira, near São Paulo, have been mentioned above (Fig. 1).

D. sturtevantii proved to be the commonest species on the island of Marajó, the second commonest in Pará, the third commonest in Maranhão, fairly common in the state of São Paulo, but not found at all in southern Brazil (Paraná and Rio Grande do Sul). Its food preferences include the jaca fruit (*Artocarpus integrifolia*) which is avoided by the *willistoni* group. In a fruit orchard at Palmares, territory of Acre, 666 of the 923 *Drosophila* caught on jaca were *D. sturtevantii* and there were no *willistoni*, while among the 300 flies collected on mango a few metres away only 53 were *sturtevantii* and 74 were *willistoni*. *D. sturtevantii* made up nearly 50% of the population of the sugar-cane juice fermenting tank at Imperatriz, Maranhão, which was also free of *willistoni*.

The *cardini* group contains *D. polymorpha*, *D. cardinoides*, *D. campestris* and *D. neocardini*. One or more of these species occur in every region and in almost every locality in Brazil where collection has been made. However, *D. polymorpha* and *D. cardinoides* are the only species of this group which occur in southern Brazil, and they are also commonest in Pará where all four species are recorded. But *D. campestris* is the commonest representative of the group in the drier regions—Goyaz, caatingas of Bahia, Maranhão, the interior of São Paulo, and, paradoxically, in Rio Negro (the Rio Negro form may be a different species).

D. simulans, and its much less common relative *D. melanogaster*, are in all probability not indigenous in Brazil. Nevertheless, *D. simulans* is widespread and is occasionally abundant in natural environments in places remote from human habitation. It is the most

abundant, or the second most abundant, species in the interior and on the plateau of São Paulo during the cooler season. In Amazonia its distribution becomes spotty and confined to fruit orchards, in some of which it is, however, present in great numbers. *D. ananassae* is certainly an introduced species commonly found near human habitations but rare or absent in natural environments. In Amazonia it is the commonest household species. *D. mirim*, the smallest species of the genus in body size, is probably a native species which nevertheless thrives in the company of introduced scavengers (*D. simulans*, *D. melanogaster* and *D. ananassae*). In 20 of the 36 samples in which *D. mirim* was present, one or more of the scavenger species were present also.

The *calloptera* group contains *D. calloptera* Schiner and at least three other undescribed species. Although these species are attracted to banana bait they fail to develop on standard laboratory media. In natural habitats they occur especially on fruits and other vegetable remains in advanced stages of decomposition which are no longer very attractive to other *Drosophilae*. Thus, species of the *calloptera* group were found abundantly on old *Bertolettia excelsa* shells in Amazonian forests and on almost dried out babasú palm seeds (*Orbygnia* sp.) in Maranhão.

D. prosaltans is one of the rare species which occurs in many parts of Brazil; but usually is found in single specimens. It is, nevertheless, common in some localities, at least in some seasons. Most striking has been its presence as the second or third commonest species in five samples from the north-eastern part of Marajó Island, near Cape Maguari. Other unusually good catches of *D. prosaltans* were made in some samples near Imperatriz, Maranhão, and in a narrowly circumscribed neighbourhood near Bertioga, on the coast of São Paulo. Banana bait several days old appears to be more attractive to this species than more freshly prepared bait.

6. SPECIES DIVERSITY

The amount of collecting in different parts of Brazil has been very unequal, and many species, especially in the equatorial zone, remain undescribed. Exact comparisons of numbers of species in tropical and temperate environments are, accordingly, impossible and only very general features of the situations can be discussed at present.

The 'caatingas' of Bahia showed the lowest species diversity among our seventeen regions of Brazil. Only five indigenous species (*nebulosa*, *pattersoni*, *cardinoides*, *mirim* and a member of the *repleta* group), and one presumably introduced one (*simulans*) were found common there, and eight additional species occurred rarely. The 'caatingas' are a semi-desert environment, where most plants lose leaves and

become dormant during the prolonged dry season, which is beyond the toleration limit of most *Drosophila* species. Conversely, the rain forests of the equatorial zone offer a variety of habitats suitable for *Drosophila*; 38 species and species groups (not including collections on fungi) have been found in the vicinity of Belem, Pará. The records for other regions are intermediate between these extremes. About 20 species and species groups are found in most samples taken in the state of São Paulo (see Table 4), and about 30 are recorded in the aggregate of samples in each of the three collecting regions in that state.

The number of species in a sample depends not only upon the species diversity in the territory where the sample is taken but also on the size of the sample. Large samples are likely to include rare species absent in small ones, and hence a greater total number of species (Fisher, Corbet & Williams, 1943; Preston, 1948). Thus, Patterson (1943) found 47 species of the genus *Drosophila* among 673,020 individuals in the state of Texas, but only 20 species among 2253 flies from the neighbouring state of Oklahoma, 18 species among 4320 flies in Arkansas, and 21 species among 18,288 flies in Louisiana. The diversity of environments in which samples are taken in a given region evidently influences the observed species diversity. Among 141,126 individuals collected on an area about 30,000 sq.m. near Austin, Texas, Patterson (1943) records only 31 species in 233 samples taken from July 1938 to May 1941. His monthly collecting totals are from 45 to 23,619 flies and from 4 to 17 species. The samples from Brazilian localities recorded in Table 4 in this article contain from 266 to 16,455 flies and 9 to 28 species and species groups. Since a 'species group' may contain several species, it is fair to say that the species diversity in Brazil is at least twice as high as in Texas. This conclusion is strengthened if we recall that Brazilian records do not include most fungus-feeding species (the North-American fungus-feeding species seem to be, on the whole, more prone to come to banana bait than are many of the Brazilian fungus feeders).

7. DISCUSSION

Two or more species or varieties having identical ecological characteristics cannot coexist indefinitely in the same territory, because one of them will prove somewhat more efficient than the others, and will outbreed and supplant its weaker competitors. This principle, formulated by Gause (1934) and elaborated especially by Lack (1947), leads to the inference that sympatric species or strains either occupy different habitats within the same territory, or exploit the same habitat in different ways, which in the last analysis, amounts to the same thing: each form of life exploits some 'ecological niches', in at least one of which it

has a net superiority over all competitors. Presence of unoccupied or inefficiently exploited ecological niches constitutes a challenge to which organisms may respond by evolutionary changes that permit them to occupy these niches. To acquire and maintain a hold on a habitat, the occupant must possess a genotype the adaptive value of which in that habitat is superior to other genotypes. Different habitats require, however, different genotypes for most efficient exploitation. A multiplicity of habitats in a given territory makes possible coexistence of sympatric forms of life.

A variety of sympatric forms sufficient to exploit the opportunities offered by a territory may be engendered in the process of evolution in two ways. First, there may appear a group of related but distinct species, each adapted to control a single or a few habitats. Secondly, a species may develop adaptive polymorphism, and come to consist of a variety of interbreeding genotypes which possess highest adaptive values in different habitats. The first method will be advantageous if the genotypes which are adaptive in different habitats are so highly integrated systems of genes that Mendelian recombination in the hybrids leads to appearance of many adaptively inferior gene patterns. Reproductive isolation of the adaptive genotypes is then favoured by natural selection, and speciation is the result. The second method is advantageous when recombination leads to no loss of reproductive potential, and too rigid a fixation of adaptive genotypes reduces evolutionary plasticity.

Both methods of adaptation to environment containing a diversity of habitats have been used in evolution of *Drosophila*. The Brazilian fauna contains common, widespread, and nutritionally versatile species like *D. willistoni*, *D. nebulosa* and *D. paulistorum*. On the other hand, such species as *D. prosaltans*, *D. bandeirantorum*, *D. pallidipennis*, *D. fumosa*, *D. nigricruria*, and others, are common only in some environments or at some seasons. It has been shown in the present article that a community of sympatric species of *Drosophila* reacts to local and to seasonal variations in the environment by changes in the relative frequencies of constituent species. We hope to show in another publication that at least some of the species that are common and ecologically versatile possess elaborate systems of adaptive polymorphism; and that rare and specialized species tend to be relatively uniform genetically within a population of each locality, although they may show considerable geographic differentiation. Polymorphic species may react to environmental variations by adaptive changes in the relative frequencies of the constituent genotypes (Dobzhansky, 1949).

Biologically the most significant difference between tropical and temperate zone environments is that the former contain a greater diversity of adaptive niches

than the latter. In response to this diversity, most groups of organisms are represented in tropical faunas and floras by greater numbers of species than in temperate or cold zone ones. Tropical environments present more numerous challenges to which organisms may respond by adaptive modifications than do temperate or cold zone environments. The diversification of organisms in the tropics is, in a way, a self-accelerating process, because the greater is the variety of organisms that live in a territory, the more complex becomes the environment and the more numerous are the challenges to which adaptive responses may be given.

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9. SUMMARY

1. Samples of *Drosophila* populations have been taken in 35 localities in 17 bioclimatic regions of Brazil. The techniques of collecting consisted in attracting the flies to bait of fermenting banana and procuring them on natural bait of fallen fruits, flowers, or other vegetable substances.

2. Samples taken at distances even as small as 10–20 m. from each other often contain different relative frequencies of various species of *Drosophila*. *Drosophila* populations thus form nuclei of high and low population densities. Some species tend to form discrete nuclei, and others to be distributed relatively more uniformly.

3. Species of *Drosophila* differ in food preferences, and some species are more specialized than others.

4. Repeated collecting within a locality discloses

the occurrence of changes in relative frequencies of different species from month to month. It is an open question to what extent these changes are cyclic and how regularly they are repeated in different years. Temporal changes occur both in regions in which dry seasons alternate with wet ones and in regions which have relatively uniform superhumid tropical climates.

5. Tropical faunas of *Drosophila* are richer in species than temperate or cold zone faunas. Within the tropics, rain forests have richer faunas than do more arid regions. The richness of tropical faunas and floras is considered to represent an adaptive response of the living matter to the diversity of habitats available in most tropical environments.

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