International Journal of Entomology Vol. 25, no. 2–3: 142–151 27 October 1983

DROSOPHILIDAE FROM BANANA TRAPS OVER AN ALTITUDINAL TRANSECT IN PAPUA NEW GUINEA

II. Frequency of species at eight collecting sites

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Abstract. Forty-six species of Drosophilidae were recorded from 8 altitudinal sites in the Morobe Province, Papua New Guinea, in 1977. Collections were made from close to the summit of Mt Kaindi (2200 m) to near sea level at Lae. Sites were established in native forested areas and each was baited with 6 small cans of fermented banana. Using males only, 3608 specimens were identified from these collections. The frequency of each species at each locality is given: sharp changes in composition occur with altitude and no species occurs at all 8 sites. A number of cosmopolitan species are apparently absent from Morobe Province; these include *D. melanogaster, D. simulans, D. hydei, D. busckii* and *D. funebris.* Only 5 specimens of the worldwide species *D. immigrans* were obtained; 4 of these came from high-altitude areas forested with *Nothofagus* and *Castanopsis.* It is suggested that this may represent an ancestral endemic population from which the worldwide forms have evolved.

New Guinea is a vast, ecologically complex tropical island that still harbors many biological unknowns. Indeed, the recent 2-volume work edited by Gressitt (1982) represents only a beginning for many fields. The Drosophilidae of the island have received almost no attention. Thus, our 1977 survey of the drosophilid fauna in a small segment of the Morobe Province, Papua New Guinea (Carson & Okada 1982), was in every sense preliminary.

As is well known, the family Drosophilidae is useful in modern biology for formal cytological and molecular genetic studies. For these studies, the cosmopolitan species *Drosophila melanogaster* Meigen has been the species of choice (Ashburner et al. 1976–1981). Less widely realized is the fact that the family is a rich source of basic information and paradigms of systematic and evolutionary biology. In the first of a series of volumes dealing with this aspect of the drosophilids, Wheeler (1981) listed just over 2500 described species in the family.

The collections detailed in this paper represent a segment of the drosophilid fauna that is of particular interest to geneticists. In 1921, Sturtevant proposed that faunal surveys of *Drosophila* species could be abetted by exposing fermenting fruit in natural forested areas and collecting specimens that are attracted. Since his time, this method has become standard worldwide for obtaining quantitative population samples of drosophilid species. One of the advantages of this method of collecting is that many of the species attracted are amenable to laboratory culture. This makes possible a plethora of basic laboratory studies, especially of genetic variability, behavior, development, and hybridization.

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The collections reported in this paper represent an attempt to find out which of the New Guinea species may be especially useful for future genetic studies. To this end, we report here on 46 species of the family that are attracted to a single artificially-yeasted fruit, the domestic banana. We are well aware that such a population sample is somewhat biased. Indeed, in a series of recent papers (Carson & Okada 1980, 1982b; Okada & Carson 1980, 1982) we have reported that many species of New Guinea drosophilids feed on and breed in flowers. Most of these species, although abundant in flowers at the same sites where the present banana-trapping was done, are not attracted to baits. In addition, we have obtained many additional species by general sweeping, mushroom baits, and light traps (Carson & Okada 1982a). There is surprisingly little overlap in the species composition of the samples taken by these different methods. As in other areas of the world, a proper total faunal survey would require using all of these methods.

Trapping of flies attracted to banana-baited lures was carried out at 8 sites in Morobe Province (Fig. 1) over an altitudinal transect running from sea level near Lae to the summit of Mt Kaindi above the village of Wau at about 2300 m altitude. The linear distance from Lae to Mt Kaindi is about 85 km. In this paper we report the frequency of those species attracted to banana at these 8 sites. Descriptions of the 15 new species encountered and systematic notes on previously-described species have been reported in the preceding paper of this series (Okada & Carson 1983).

MATERIAL AND METHODS

The species collected are listed in Tables 1 and 2, along with other pertinent information on each species. At almost every site, a small number of specimens of additional undescribed species were obtained. Primarily because of the paucity of this material, we have chosen not to deal with it in this and the preceding paper. Rather, we have concentrated on the more abundant material or on species that appear to be of special systematic or genetic interest. Thus, the *melanogaster* group, which includes 19 of the 20 *Drosophila* (*Sophophora*) species found, has received special attention. This large group is of great evolutionary interest (see Bock & Wheeler 1972).

Since females of many species are morphologically cryptic, all our frequency data are based on males only, although in a number of instances we have added the results of so-called "isofemale" cultures. Thus, from each site, 15 to 30 wild-caught females were placed individually into separate culture tubes of standard instant *Drosophila* medium and allowed to produce progeny in the laboratory. As well as providing cultures for use in genetic crosses, such purebred lines provide a good source of material for systematic study. Each isofemale line provides for certain identification of F_1 males. Accordingly, each such line has been used to add 1 male each to the census of wild males at each site. Tables 1 and 2 (right-hand columns) give estimates of the success of isofemale line production for each species. Despite their attraction

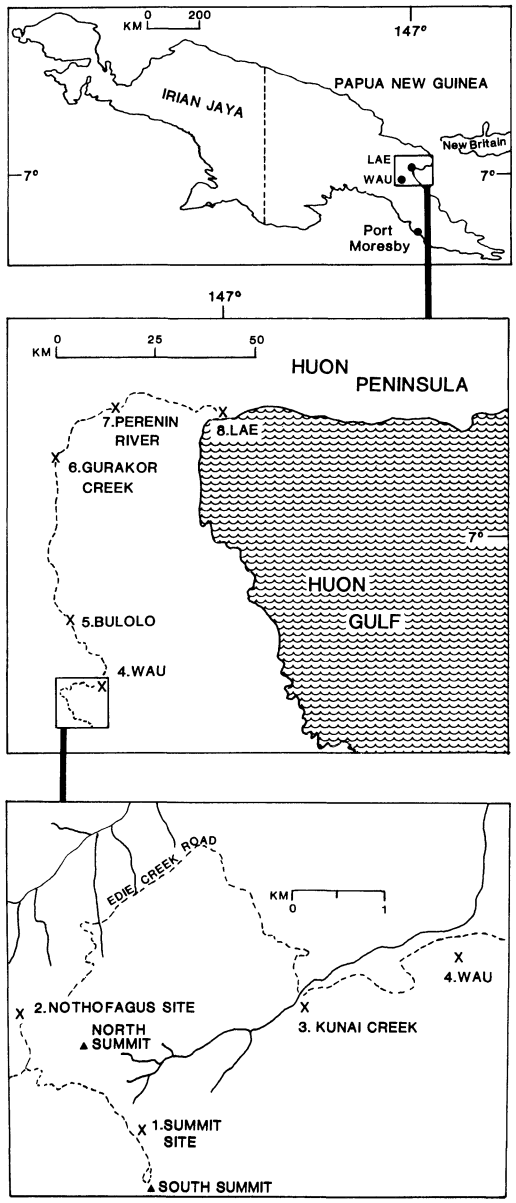

FIG. 1. Locations of the collecting sites. Upper: location of Papua New Guinea; the boxed area is the relevant portion of Morobe Province, including Lae and Wau. Middle: enlargement of the boxed area between Lae and Wau, showing the positions of collecting sites 4 through 8. Bottom: enlargement of the area of Mt Kaindi, above Wau. The positions of sites 1 to 4 along Edie Creek Road are shown.

TABLE 1. Authorities and subgroups for *Drosophila* (*Sophophora*) species listed in Table 3. All but *unguicula* belong to the *melanogaster* species group.

SPECIES (=20)	AUTHORITY	SUBGROUP OR REMARKS	ISO-♀ LINE PRODUCTION
ananassae	Doleschall 1858	*ananassae*	yes
apodemata	Okada & Carson 1983	*suzukii*	unknown
bipectinata	Duda 1923	*ananassae*	yes
birchii	Dobzhansky & Mather 1961	*montium*	yes
constricta	Okada & Carson 1983	unknown	yes
denticulata	Bock & Wheeler 1972	*denticulata*	yes
eugracilis	Bock & Wheeler 1972	*eugracilis*	few offspring
gorokaensis	Carson & Okada 1982	*ficusphila*	yes
hypomelana	Okada & Carson 1983	*suzukii*	no
ironensis	Bock & Parsons 1978	*ananassae*	unknown
kikkawai	Burla 1954	*montium*	yes
longissima	Okada & Carson 1983	*montium*	few offspring
mayri	Mather & Dobzhansky 1962	*montium*	yes
pseudoananassae	Bock 1971	*ananassae*	yes
pseudomayri	Baimai 1970	*montium*	yes
pseudotakahashii	Mather 1957	*takahashii*	yes
rhombura	Okada & Carson 1983	*montium*	unknown
rhopaloa	Bock & Wheeler 1972	*montium*	unknown
serrata	Malloch 1927	*montium*	yes
unguicula	Okada & Carson 1983	*dispar*	unknown

to banana, members of the subgenus *Scaptodrosophila* are very difficult to rear in this manner.

The biogeography and ecology of the altitudinal transect along which the collections were made has been ecologically plotted (Gressitt & Nadkarni 1978). Each of the 8 sites chosen consisted of a reasonably intact forest ecosystem along the road leading from the S summit of Mt Kaindi and from the gold-mining area of Edie Creek down through Wau and Bulolo to Lae at the Huon Gulf on the NE coast. Except at Bulolo, each area was within 100 m of the road.

Starting at the S summit of Mt Kaindi, the following sites, numbered 1–8 in Fig. 1 and Table 3, were selected. A short name designation in parentheses below is given to each site. Each is recorded as being on the right-hand or left-hand side of the road as one proceeds from the S summit of Mt Kaindi (2362 m) to Lae.

1. Mt Kaindi (*summit site*). 2200 m. The site is N of the S summit along a well-used forest trail that leads NE from the right-hand side of the road at a point just S of the Omas house (see Gressitt & Nadkarni 1978, Fig. 47). Denoted the "contour trail," it runs at approximately 2200 m elevation around the S summit. This is upper montane zone, with substantial native forest, including *Nothofagus carrii* and *N. pullei*. 6 traps; 5 collections: 28.VIII–12.IX.1977.

2. Mt Kaindi (*Nothofagus site*). 2120 m. The road to Lae skirts the northern side of the N summit and then bends to the right just before descending sharply. The

TABLE 2. Authorities and subgroups for *Drosophila* (*Scaptodrosophila*), *Drosophila* (*Drosophila*) and for 3 other genera.

	AUTHORITY	SUBGROUP OR REMARKS	ISO-♀ LINE PRODUCTION
Subgenus *Scaptodrosophila* (=10)			
ambiguifasciata	Okada & Carson 1983		unknown
elutoides	Okada & Carson 1983		unknown
latifasciola	Okada & Carson 1983		unknown
nannosoma	Okada & Carson 1983		no
novoguineensis	Duda 1923		poor
paranthia	Okada & Carson 1982		unknown
parapunctipennis	Duda 1924		unknown
specensoides	Okada & Carson 1983		die as pupae
spinomelana	Okada & Carson 1983		no
subeluta	Okada & Carson 1983		unknown
Subgenus *Drosophila* (=11)			
alpiniae	Okada & Carson 1980	*melanderi*	no
argentostriata	Bock 1966	=*Zaprionus* or *Phorticella*?	poor
crispipennis	Okada & Carson 1983	*immigrans*	yes
hypocausta	Osten-Sacken 1882	*immigrans*	yes
immigrans	Sturtevant 1921	*immigrans*	yes
niveifrons	Okada & Carson 1983	*immigrans*	yes
persicae	Bock & Parsons 1978	unknown	unknown
rubida	Mather 1960	*immigrans*	yes
silvistriata	Bock & Baimai 1967	=*Zaprionus* or *Phorticella*?	few offspring
sulfurigaster	Duda 1923	*immigrans*	yes
tetrachaeta	Angus 1964	*immigrans*	poor
Other species (=5)			
Phorticella flavipennis	Duda 1929	=*Zaprionus*?	unknown
Sphaerogastrella novoguinensis	Duda 1929		no
Styloptera maculata	Carson & Okada in Okada 1982		yes
S. punctata	Okada & Carson 1983		unknown
S. tigrina	Carson & Okada in Okada 1982		unknown

collection site is to the left of the road in an area of upper montane zone dominated by a grove of very large *Nothofagus grandis* trees. 6 traps; 7 collections: 10–27.X.1977.

3. Mt Kaindi (*Kunai site*). 1515 m at the point where Kunai Creek crosses the road. The site of placement of the lures was in the mid-montane zone up a steep slope on the right of the road in an extensive grove of *Castanopsis* and *Elaeocarpus* trees. 6 traps; 7 collections: 5, 8–14.IX.1977 and 2, 1–2.XI.1977.

4. Mt Kaindi (*Wau site*). 1200 m on right side of road in the mid-montane zone. The specific site was in a remnant of virgin forest on the property of the Wau Ecology Institute, about 200 m downslope from the main Institute buildings. The site is locally known as the "bird of paradise display area," since it has been long frequented by *Paradisaea raggiana*. 6 traps; 3 collections: 22–24.IX.1977.

5. Headshump Forest (*Bulolo site*). 910 m. This site is a special experimental forest preserve. It is dominated by large *Araucaria* trees, representative of lower montane zone. The tract is located about 8 km N of the town of Bulolo to the right of the road as one nears the town. It is situated about 180 m higher than the town itself. 6 traps; 2 collections: 17–18.IX.1977.

6. Gurakor Creek (*Gurakor site*). 610 m. The site is located upstream (right-hand side of road) just at the point where the road crosses the creek. Baits were placed in hill forest zone, specifically a gallery forest along a trail which follows up the creek. 6 traps; 1 collection: 5.XI.1977.

7. Perenin River (*Perenin site*). 227 m. The site is on the left-hand side of the road, about 2 km before the road crosses the river. Baits were placed in dense hill forest zone on the high bank of the river. 6 traps; 2 collections: 5,7.XI.1977.

8. Lae Botanical Garden (*Lae site*). 10 m. The garden itself includes several well-preserved natural hillsides and areas characteristic of the lowland rainforest zone. These are within a 5-minute walk from the Huon Gulf Motel at Lae. Baits were placed in the dense forest on these slopes. 6 traps; 2 collections: 28–29.IX.1977.

Each bait setting consisted of 6 metal cans (9 cm in diam. and 14 cm long; capacity 450 ml). In the bottom of each can was placed about 100 ml of mashed banana pulp without skins and some absorbent paper. The bait had been inoculated with bakers' yeast and allowed to ferment for 2 days in a bucket before use. The lures were spaced at least 40 m apart. Each was suspended by a string from a tree branch and was fitted with a folded and inverted paper plate which served as a roof to exclude rain (see Fig. 3, p. 684 of Gressitt 1982). The suspending strings were greased with petroleum jelly mixed with insect repellent to keep ants from reaching the bait.

Collections were begun 1–2 days after setting by using a rigid sleeve of clear plastic fitted at 1 end with a plastic bag. This unit was clapped over the trap and flies moving into the plastic bag were aspirated and placed alive onto food vials. They were taken to the laboratory in an insulated box, where they were sorted and identified. Isofemale lines were established. Trap visitations were more frequent at localities 1–3, but this does not appear to have affected the numbers of species obtained at each site.

RESULTS

The basic data are recorded in Table 3. Species have been grouped into 3 main subgenera. Within each subgenus, the order of the species reflects those found to be most numerous at the higher altitudes.

Of the 46 species present, 10 are represented by less than 5 males each. One would be tempted to list such species as "rare" were it not for the fact that their paucity may be due partly to their failure to be attracted to banana bait. This is clearly true for some of the species, which may be obtained in substantial numbers by general sweeping, e.g., *D. alpiniae* and *D. tetrachaeta.*

D. rubida, D. hypocausta, D. sulfurigaster and *D. pseudomayri* appear to have the

TABLE 3. Number of males of 46 species of Drosophilidae collected at banana baits at 8 altitudinal sites in Morobe Province, Papua New Guinea in 1977. See Tables 1, 2 and text for further details.

SITE NO.:	SUMMIT 1	*Nothofagus* 2	KUNAI 3	WAU 4	BULOLO 5	GURAKOR 6	PERENIN 7	LAE 8	
ALTITUDE (M):	2200	2120	1515	1200	910	610	227	10	TOTALS
Drosophila (*Sophophora*) (=20)									
hypomelana	41	230	—	—	—	—	—	—	271
pseudomayri	25*	89	212	6*	5*	4	—	—	341
gorokaensis	18*	165	23*	—	—	—	—	—	206
pseudotakahashii	3	39	359*	6*	—	—	—	—	407
unguicula	5	—	1	—	—	—	—	—	6
rhombura	1	2	11	†	—	—	—	—	14
apodemata	—	—	1	—	—	—	—	—	1
mayri	—	—	1	10*	3*	2	9*	—	25
eugracilis	—	—	1	14*	—	2*	2	13*	32
denticulata	—	—	1	1	1	—	2	1*	6
ironensis	—	—	1	—	—	—	11	1	13
rhopaloa	—	—	2	—	—	—	—	—	2
pseudoananassae	—	—	—	10*	7*	18*	9*	10*	54
ananassae	—	—	—	8*	10*	10*	28	80*	136
birchii	—	—	—	8*	4	4*	1	1	18
serrata	—	—	—	5	3	—	—	—	8
kikkawai	—	—	—	1	—	—	—	—	1
longissima	—	—	—	1*	—	—	—	—	1
bipectinata	—	—	—	—	1*	1*	5*	3	10
constricta	—	—	—	—	—	12*	14*	—	26
Total									1578
Drosophila (*Scaptodrosophila*) (=10)									
spinomelana	21	6	—	—	—	—	—	—	27
specensoides	7	70	280	118	—	1	1♀	—	477
novoguineensis	—	—	6	184	43	1	7	1	242
subeluta	—	—	†	6	—	—	—	†	6
latifasciola	—	—	—	7	—	—	—	—	7
parapunctipennis	—	—	—	1	1	2	1	1	6
ambiguifascia	—	—	—	—	5	—	—	—	5
nannosoma	—	—	—	—	—	25	15	37	77
elutoides	—	—	—	—	—	—	—	2	2
paranthia	—	—	—	—	—	—	—	3	3
Total									852

TABLE 3. Continued.

SITE NO.:	SUMMIT 1	*Nothofagus* 2	KUNAI 3	WAU 4	BULOLO 5	GURAKOR 6	PERENIN 7	LAE 8	
ALTITUDE (M):	2200	2120	1515	1200	910	610	227	10	TOTALS
Drosophila (*Drosophila*) (=11)									
alpiniae	6	—	—	—	—	—	—	—	6
immigrans	—	2*	2	1♀†	—	—	—	—	4
crispipennis	—	1	23*	1	—	—	—	—	25
hypocausta	—	—	27	213	8	5	12	5	270
rubida	—	—	9	81	78	65	103*	5	341
sulfurigaster	—	—	4	95*	13*	13	18	97*	240
silvistriata	—	—	3	43	14	—	4	—	64
argentostriata	—	—	—	83	—	—	—	—	83
tetrachaeta	—	—	—	1	—	—	—	—	1
niveifrons	—	—	—	3	4*	2	17	15*	41
persicae	—	—	—	—	—	—	—	11	11
Total									1086
Phorticella flavipennis	—	—	—	3	—	—	—	—	3
Sphaerogastrella novoguinensis	—	—	—	†	—	—	—	1	1
Styloptera									
maculata	—	—	5	6	2	46*	5*	17	81
punctata	—	—	3	—	—	1	—	—	4
tigrina	1	1	1	—	—	—	—	—	3
Total									92
No. species	10	10	22	29	17	18	19	20	46
No. ♂	128	605	976	915	202	214	264	304	3608

* Includes 1 or more iso-♀ lines in which the species was identified from F_1 ♂ specimens.
† Species recorded from area but not at banana traps.
♀ = ♀ specimen only.

greatest altitudinal range, although no single species is present at all 8 collecting localities. The Wau site appears to be the richest in species (29), even though only 3 collections were made there. This probably reflects the richness of the mid-montane zone but is possibly also affected by the proximity of the site to the orchards, gardens and arboreta of the Wau Institute. A number of striking cases of localization are apparent (e.g., *D. argentostriata, D. hypomelana,* and *D. unguicula*). *D. novoguineensis* appears to have a peak abundance at moderate altitudes.

Several distinct surprises deserve comment. Carson (1965) and Parsons & Stanley (1981) have listed 8 species of the genus *Drosophila* as virtually cosmopolitan. Prominent among these are *D. melanogaster, D. simulans, D. busckii, D. hydei* and *D. repleta.* Except for *repleta,* which did not come to banana bait, none of these has been recorded from Morobe Province. *D. melanogaster,* however, was first collected in New Guinea by one of us (T.O.) on October 13, 1977 on the S side of the island near Port Moresby. Earlier (1961) collections made by one of us (H.L.C.) on both sides of the island showed an absence of this species and suggests that it has only recently been introduced into New Guinea and has not yet reached the Morobe Province.

The very great rarity of *Drosophila immigrans* Sturtevant, a species which is abundant in banana traps almost everywhere in the world, needs comment. As the nominate species of the large *immigrans* group of the subgenus *Drosophila,* it has many relatives in New Guinea and in the Oriental Region (see Table 2). The same, of course, is true of *D. melanogaster*: 19 species of the *melanogaster* group are found on this transect.

We have recognized only 5 specimens of *D. immigrans* in our collections; 4 were caught in the montane zone on Mt Kaindi. A single female specimen was obtained in general sweeping at Wau (see Table 3). Two males and 1 female from the *Nothofagus* site were used to establish a laboratory stock (K-30), which was taken to Australia in December 1977 by H.L.C. and given to Dr I.R. Bock of LaTrobe University, Melbourne. He identified the culture as *D. immigrans* Sturtevant by study of male genitalia. The chromosomes of this strain were determined to be homozygous for the standard sequences by Tribe (1981). Such homozygosity, even for 2 flies, would be a rarity elsewhere in the world.

Clearly, further study of *D. immigrans* populations in the high altitudes of New Guinea is much needed. We may cautiously suggest, however, that we may be observing here an endemic population of the species. It may represent the true ancestor of the worldwide cosmopolitan form. The existence of such endemic ancestors for cosmopolitan forms was predicted by Carson (1965).

To complete comments on the status of the 8 cosmopolitan species in Morobe Province, it may be said that the only cosmopolitan species abundantly found on the Morobe transect is *D. ananassae*; it occurs in substantial numbers at lower elevations. Everywhere it is accompanied by the sibling species *D. pseudoananassae,* which occurs in numbers about equal to *D. ananassae.* The latter, however, predominates at the 2 lowest collecting sites. The final member of the "cosmopolitan 8" is *D. funebris.* It also has not been recorded from New Guinea.

Ordinarily, few flies other than those belonging to the genus *Drosophila* are attracted to banana traps. Accordingly, the presence of *Styloptera maculata* in these collections, with a wide altitudinal range, is of special interest. The genus is not well known; indeed, until our recent work, it was a monotypic genus, having been established for *S. formosae* Duda (Okada 1982).

Acknowledgments. This work was carried out with the aid of a Japan (JSPS)–United States (NSF) Cooperative Science Program Grant (INT 76-82440). We thank Dr I.R. Bock for identifying *D. immigrans* and for valuable comments. Meredith S. Carson gave valuable support in the field and laboratory. The authors have dedicated this and the preceding paper to the memory of J. Linsley Gressitt and Margaret Gressitt.

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