

*Kontyû, Tokyo*, 45(4): 571-582. December 25, 1977

## Breeding Sites of Drosophilid Flies in and near Sapporo, Northern Japan, with Supplementary Notes on Adult Feeding Habits

Masahito T. KIMURA, Masanori J. TODA, Katsura BEPPU  
and Hide-aki WATABE

Zoological Institute, Faculty of Science, Hokkaido University  
Sapporo, Hokkaido 060, Japan

**Synopsis** As breeding sites for drosophilid flies, four types of substrates, fermenting fruits, decayed leaves, slime fluxes, and fleshy fungi, were recorded in and near Sapporo. The breeding habits of drosophilid flies are discussed in relation to their phylogeny.

Information on breeding sites of drosophilid flies is indispensable for their ecological and evolutionary studies (CARSON and STALKER, 1951; etc.). Reviewing previous contributions, CARSON (1971) classified the various breeding substrates so far known into seven categories: 1) fallen fruits and flowers, 2) slime fluxes, 3) decayed bark, leaves, stems or roots, 4) fleshy fungi, 5) living leaf tissue (leaf miner), 6) living flowers, and 7) symbionts. Of these seven, the first five are known to be utilized in temperate regions (FROST, 1924; CARSON and STALKER, 1951; OKADA, 1968; etc.). However, only fragmentary records of the breeding sites of drosophilid flies are known for Hokkaido (MOMMA, 1965; KIMURA, 1976a). The present paper reports the results obtained through surveys carried out for the five years since 1972 in and near Sapporo, together with discussion on the relationships between the phylogeny and breeding habits of drosophilid flies.

Before going further the authors wish to express their cordial thanks to Professor Eizi MOMMA and Dr. Shôichi F. SAKAGAMI for their pertinent guidance in the course of the present study and for reading through the manuscript.

### The Area Surveyed and Methods

The area surveyed, Sapporo (43°N, 141°E), is located near the northern edge of the primary temperate deciduous forest, which is replaced on upland margins by forests admixed with conifers. The highest and lowest monthly mean temperatures are about 21°C (August) and -5°C (January). The active season of drosophilid flies runs from April to November, the remaining months having deep snow.

In order to obtain information about breeding sites, various organic materials suspected to contain larvae or eggs were collected in the field, and brought to the laboratory. Samples were sorted by the kinds of materials, e.g., species of fungi or plants. Each sample was placed in a milk bottle (180 ml) with tissue paper at the

bottom and a cotton plug at the mouth, and stored at a room temperature (18~24°C). Adults reared from the substrates were collected by an aspirator and were identified by species.

In addition to the survey of breeding substrates, adult flies attracted to such substrates were collected by net sweeping to obtain information on adult feeding habits.

## Results

### *Breeding substrates*

In total, ninety kinds of organic materials and some unidentified plants were confirmed as being utilized for breeding (see Appendix I). They were classified into four categories, fermenting fruits and hulls, slime fluxes (fermenting tree sap), decayed leaves and stems, and fleshy fungi, which are henceforth abbreviated as **F**, **T**, **L**, and **M**. 1) **F**: Four wild fruits, three cultured ones and two wild hulls were utilized for breeding. But these substrates would be subsidiary at least in Hokkaido, where wild fruiting plants are few, and the fruiting season is generally late autumn after the breeding season of most wild fly species is terminated (TODA *et al.*, unpubl.). 2) **T**: Slime fluxes of eight species of broad leaved trees were confirmed as breeding sites, mostly produced by felling trees except for the natural slime production of *Ulmus davidiana* var. *japonica*. TODA (1973) reported *D. moriwakii* breeding on slime fluxes of wounded plant roots on a small cliff in a forest felling area. A similar situation was also recorded for several species, and in addition, on logs in a timberyard. In both cases, the tree species were not identified, and each of them is therefore counted as one unit in Table 1 and Appendix I. 3) **L**: Decayed leaves and stems are divided into  $L_1$  of herbaceous plants (18 species), and  $L_2$  of unidentified arboreal plants which have drifted to river shores. 4) **M**: Forty-four species of fleshy fungi belonging to Agaricales and eleven species of Aphyllophorales were observed to be used as breeding sites.

### *Breeding habits*

Of the 103 drosophilid species so far recorded in Hokkaido (BEPPU *et al.*, 1977), 42 species were reared in the present study. The data are presented for each species in Appendix II, with records of adults collected. Specific breeding habits are expressed in Table 1, based upon the relative importance of the numbers of plant species utilized among the four types of breeding sites mentioned above. Where the number of utilized species forms a high proportion of the total species of a particular breeding site, this means, in general, the importance of such a site for fly species concerned. The comparison of the number of individuals reared from each substrate is rather meaningless, as the collections of breeding substrates were not carried out quantitatively and the culture was not made under constant conditions.

Next, the breeding habits of each species are mentioned for each radiation of the phylogeny according to THROCKMORTON (1975).

The Steganine Radiation: Breeding sites of the subfamily Steganinae are little known. Only one individual of *Amiota variegata* D type was reared from T. *Leucophenga maculata* and *L. quinquemaculipennis* were observed breeding on M.

The *Scaptodrosophila* Radiation: *Drosophila coracina* and *D. throckmortoni* were reared from T.

The Sophophoran Radiation: *Drosophila bifasciata* of the *obscura* group utilized T as the main breeding site, including one specimen reared from M. One species of the *mommai* group, *D. mommai*, bred on L<sub>1</sub>. The members of the *melanogaster* group are divided into two types by breeding habits. One is represented by two species of the *nipponica* subgroup, *D. nipponica* and *D. magnipectinata*, breeding on L<sub>1</sub>, and the other is fruit breeders, *D. lutescens*, *D. suzukii*, *D. auraria*, *D. biauraria*, and *D. melanogaster*, though the last three also utilized, in a subsidiary way, substrates other than fruits.

The *Drosophila* Radiation: Two species of the *funnebris* group, *D. funnebris* and *D. multispina*, bred on M.

The *virilis-repleta* Radiation: *Drosophila ezoana* of the *virilis* group, and *D. lacertosa*, *D. moriwakii*, *D. sordidula*, *D. pseudosordidula*, *D. okadai*, and *D. neokadai* of the *robusta* group mainly bred on T. It is noteworthy that the last two species were observed breeding on the decayed leaves and stems which had drifted on river shores (L<sub>2</sub>).

The *immigrans* Radiation: *Drosophila immigrans*, *D. nigromaculata*, and *D. testacea* utilized a variety of substrates, though each species had only one main breeding site: *D. immigrans* for F, *D. nigromaculata* for L<sub>1</sub> and *D. testacea* for M. *Drosophila brachynephros*, *D. unispina*, *D. histrio*, and *D. confusa* bred on M in the main, and *D. tenuicauda* on L<sub>1</sub>.

The *Hirtodrosophila* Radiation: Three species of *Scaptomyza*, *S. pallida*, *S. consimilis* and *S. okadai*, were confirmed mainly breeding on L<sub>1</sub>, though the first two also breed, but seldom, on M or F. *Mycodrosophila poecilogastra* was observed breeding on M. The members of the *quadrivittata* group, *D. quadrivittata*, *D. trivittata*, *D. sexvittata*, *D. alboralis*, also utilized M as the main breeding site. In addition to M, *D. sexvittata* was reared from L<sub>1</sub>, and *D. alboralis* from T. *Drosophila collinella* of the subgenus *Lordiphosa* bred on L<sub>1</sub>, and *D. busckii* of the subgenus *Dorsilopha* on M and L<sub>1</sub>.

#### *Fungus preferences*

In the preceding section species-specific utilization among the four types of breeding sites was described. The following is concerned with the separation within the fleshy fungus site (M), which was most intensively surveyed among the four types of sites. Table 2 shows the numbers of species of Aphyllophorales and of each family of Agaricales used for breeding. All species referred to the table, except *D. nigromaculata*, utilized fungi as the main breeding site. They are classified into two types, A) species showing narrow preferences for fungi of Tricholoma-

Table 1. Numbers of plant species utilized by each species for breeding, separately presented for each type of breeding site, together with records of adult collections.

Types of breeding sites	Slime Fluxes(T)		Fermenting Fruits(F)		Decayed Leaves(L)			Fleshy Fungi(M)		Breeding Habits*
	B	C	B	C	L <sub>1</sub>	L <sub>2</sub>	C	B	C	
Total plant species No.	10	12	9	8	18	1		55	71	
Steganine Radiation										
<i>Amiota variegata</i> D type	1	5	—	—	—	—	—	—	1	T
<i>Leucophenga maculata</i>	—	1	—	—	—	—	—	2	5	M
<i>L. quinquemaculipennis</i>	1	—	—	—	—	—	—	4	1	Mt
Scaptodrosophila Radiation										
<i>Drosophila coracina</i>	4	8	—	—	—	—	—	—	8	T
<i>D. throckmortoni</i>	1	—	—	—	—	—	—	—	—	T
Sophophoran Radiation										
<i>obscura</i> group										
<i>D. bifasciata</i>	7	7	—	1	—	—	—	1	1	Tm
<i>mommai</i> group										
<i>D. mommai</i>	—	—	—	—	4	—	≡	—	2	L
<i>melanogaster</i> group										
<i>D. nipponica</i>	—	1	—	1	8	—	≡	—	4	L
<i>D. magnipectinata</i>	—	—	—	1	10	—	≡	—	3	L
<i>D. auraria</i>	—	1	4	4	1	—	+	1	5	Fm
<i>D. biauraria</i>	—	—	4	3	—	—	—	1	3	Fm
<i>D. lutescens</i>	—	—	2	1	—	—	—	—	1	F
<i>D. suzukii</i>	—	—	2	2	—	—	—	—	3	F
<i>D. melanogaster</i>	—	—	2	—	—	—	—	1	—	Fm
<i>Drosophila</i> Radiation										
<i>funebis</i> group										
<i>D. funebis</i>	—	—	—	—	—	—	—	2	1	M
<i>D. multispina</i>	—	—	—	—	—	—	—	2	3	M
<i>virilis-repleta</i> Radiation										
<i>virilis</i> group										
<i>D. ezoana</i>	2	3	—	—	—	—	—	—	—	T
<i>robusta</i> group										
<i>D. lacertosa</i>	2	2	—	—	—	—	—	—	3	T
<i>D. moriwakii</i>	5	8	—	—	—	—	—	—	2	T
<i>D. sordidula</i>	1	1	—	—	—	—	—	—	—	T
<i>D. pseudosordidula</i>	3	3	—	—	—	—	—	—	—	T
<i>D. okadai</i>	1	4	—	—	—	1	—	—	2	Tl
<i>D. neokadai</i>	1	—	—	—	—	1	—	—	1	Tl
<i>immigrans</i> Radiation										
<i>immigrans</i> group										
<i>D. immigrans</i>	—	1	4	3	1	—	—	2	8	Fml
<i>testacea</i> group										
<i>D. testacea</i>	4	6	—	2	5	—	+	27	40	Mlt

Table 1. (Continued)

Types of breeding sites	Slime Fluxes (T)		Fermenting Fruits(F)		Decayed Leaves (L)			Fleshy Fungi(M)		Breeding Habits*
	B	C	B	C	L <sub>1</sub>		L <sub>2</sub>	B	C	
					B	C				
Total plant species No.	10	12	9	8	18	1		55	71	
<i>quinaria</i> group										
<i>D. nigromaculata</i>	—	4	6	5	11	—	‡	6	16	Lfm
<i>D. brachynephros</i>	—	2	1	1	2	—	+	27	39	Mlf
<i>D. unispina</i>	—	—	—	2	1	—	—	22	40	MI
ungrouped species										
<i>D. histrio</i>	—	1	—	1	—	—	—	8	11	M
<i>D. confusa</i>	2	4	—	—	—	—	—	19	22	Mt
<i>D. tenuicauda</i>	—	—	—	—	6	—	‡	—	3	L
<i>Hirtodrosophila</i> Radiation										
genus <i>Scaptomyza</i>										
<i>S. pallida</i>	—	1	1	2	9	—	‡	2	3	Lfm
<i>S. consimilis</i>	—	1	—	—	5	—	‡	1	2	Lm
<i>S. okadai</i>	—	—	—	—	5	—	‡	—	1	L
genus <i>Mycodrosophila</i>										
<i>M. poecilogastra</i>	—	—	—	—	—	—	—	4	15	M
subgenus <i>Lordiphosa</i>										
<i>D. collinella</i>	—	1	—	—	9	—	‡	—	9	L
subgenus <i>Dorsilopha</i>										
<i>D. busckii</i>	—	—	—	—	2	—	—	3	—	MI
<i>melanderi</i> group										
<i>D. makinoi</i>	—	—	—	—	—	—	—	3	4	M
<i>quadrivittata</i> group										
<i>D. trivittata</i>	—	—	—	—	—	—	—	10	13	M
<i>D. sexvittata</i>	—	1	—	1	1	—	—	22	47	MI
<i>D. quadrivittata</i>	—	—	—	—	—	—	—	4	10	M
<i>D. alboralis</i>	1	1	—	—	—	—	—	25	38	Mt

B: breeding, C: adult collection, L<sub>1</sub>, L<sub>2</sub>: explained in text.

\* Breeding habits expressed by the combination of abbreviation of the four types of breeding sites, capitals: main sites, small letters: subsidiary ones.

taceae and/or Aphyllophorales: *L. quinquemaculipennis*, *L. maculata*, *M. poecilogastra*, *D. quadrivittata*, and *D. trivittata*, and B) species showing broad preferences: *D. sexvittata*, *D. alboralis*, *D. brachynephros*, *D. unispina*, *D. testacea* and *D. confusa*. Among the former group *D. trivittata* showed a clear specialization to Tricholomataceae, especially to genus *Pleurotus*, but unfortunately the other species were insufficient in their individual numbers reared to infer such specialization. Among B, only *D. confusa* seems to be specific, showing a relatively strong preference for Aphyllophorales. According to KIMURA (1976 b), all members of *Hirtodrosophila* differed for each other in their adult fungus preferences. In the present survey, however, *D. sexvittata* and *D. alboralis* showed quite similar fungus preferences for breeding. *Drosophila nigromaculata* which used L<sub>1</sub> as the main breeding site, bred mostly on fungi of Coprinaceae.

Table 2. Numbers of fungus species utilized by each species for breeding, separately shown for order Aphyllophorales and each family of order Agaricales.

Order	Aphyllophorales	Agaricales								
		Tr	Am	Ag	Co	Cr	St	Rh	Ru	Bo
Family										
Total species No.	11	19	5	2	5	2	2	2	4	3
Steganine Radiation										
<i>L. maculata</i>	2	—	—	—	—	—	—	—	—	—
<i>L. quinquemaculipennis</i>	4	—	—	—	—	—	—	—	—	—
<i>immigrans</i> Radiation										
<i>D. testacea</i>	3	7	4	1	4	1	—	1	3	3
<i>D. nigromaculata</i>	1	1	—	—	4	—	—	—	—	—
<i>D. brachynephros</i>	—	10	4	—	5	2	1	1	1	2
<i>D. unispina</i>	1	9	4	1	4	1	—	—	2	1
<i>D. confusa</i>	6	5	3	—	2	—	—	—	2	1
<i>Hirtodrosophila</i> Radiation										
<i>M. poecilogastra</i>	2	2	—	—	—	—	—	—	—	—
<i>D. quadrivittata</i>	3	1	—	—	—	—	—	—	—	—
<i>D. trivittata</i>	—	9	—	—	—	—	—	1	—	—
<i>D. sexvittata</i>	1	10	2	1	3	2	1	1	1	—
<i>D. alboralis</i>	5	9	3	—	3	1	2	1	1	—

Tr: Tricholomataceae, Am: Amanitaceae, Ag: Agaricaceae, Co: Coprinaceae, Cr: Crepidotaceae, St: Strophariaceae, Rh: Rhodophyllaceae, Ru: Russulaceae, Bo: Boletaceae

#### Adult feeding habits

The difference of feeding habits between larvae and adults is important, but hitherto little known. In Table 1 the records of adult collections are also presented. In the case of decayed leaves ( $L_1$ ), adult flies were captured by sweeping over various herbs, so that it can not be accurately decided to which plant the flies were actually attracted. Consequently, instead of plant species numbers, weighed relative abundance is tentatively shown for the species collected by sweeping. At first sight, coincidence of breeding and adult collection data is clear in the table, that is, substrates which attract adult flies of a given species are also utilized by its larvae. But a closer inspection reveals that some substrates are utilized only by adults in several species, e.g., deliquescent or decayed fungi only for adult feeding by *D. coracina*, *D. collinella* and some members of the *melanogaster* and *robusta* groups. CARSON and STALKER (1951) also observed adults of *D. robusta* feeding but not ovipositing on fungi. Slime fluxes also seem to be utilized by some species of the *immigrans* radiation only as adult feeding sites.

Two fungus-feeding species, *D. sexvittata* and *D. trivittata*, attracted to fresh fungi (KIMURA 1976 b), usually alight on lamellae of fungi and exhibit feeding behavior. The flies are considered to feed on spores which grow on lamellae. In contrast, their larvae burrow into a fungus body and are considered to feed on hyphae. CARSON *et al.* (1956) revealed the difference between yeasts isolated from

crops of adult flies of some drosophilid species and those isolated from their breeding sites. This suggests not only site separation but also separation of actual food between adults and larvae even at the same site.

### Discussion

As mentioned in the results, each of the most species mainly depend on only one breeding site among the four types. Even in several species which widely use three types they tend to select one type as the main breeding site, e.g., *D. auraria* and *D. immigrans* mainly for F, *D. brachynephros* and *D. testacea* for M, and *S. pallida* and *D. nigromaculata* for L<sub>1</sub>. On the other hand, the plant host specificity of the fly species concerned in the present study is not so rigid as in tropical oligophagous flower breeders (PIPKIN *et al.*, 1966), or many other phytophagous insects; the substrates used by each species usually extend over many plant species or even families. Although it is not known whether this versatility is due to the nature of substrates, in that all of them except for fresh fungi are fermented or decayed by yeasts or bacteria, it is certain that each fly species discriminates at least among four types of breeding sites. How they discriminate, what differences of microbe flora exist among substrates and among the types of breeding sites, and on which parts of materials (substrates, microorganisms, or their products) the larvae actually feed, require further study.

As illustrated in Fig. 1, at the level of the species group or subgenus, the breeding habits are rather uniform, though with some exceptions. Slime fluxes (T) are mainly used by the subgenus *Scaptodrosophila*, the *obscura* group, the *virilis* group, and the *robusta* group, while fleshy fungi (M) are used by members of *Leucophenga*, *Mycodrosophila*, *Hirtodrosophila* and some groups of *immigrans* radiation. These two breeding sites are also utilized by the respective relatives in other temperate regions (In Europe, BASDEN, 1954; BURLA and BÄCHLI, 1968; SHORROCKS and WOOD, 1973; and in North America, CARSON, 1951; CARSON and STALKER, 1951). Decayed leaves (L<sub>1</sub>) are utilized by members of *Scaptomyza*, *Lordiphosa*, the *nipponica* subgroup of the *melanogaster* group, and the *quinaria* group. In other temperate areas, only *D. palustris* of the *quinaria* group is known to breed on decayed water plants (North America, SPENCER, 1942). *Drosophila fenestrarum* and *D. andalusiaca* (cited as *D. forcipata*) of the *Lordiphosa* in Europe may also breed on decayed leaves, because they are collected exclusively by net sweeping on herbs as well as *D. collinella* (HERTING, 1955). In Sapporo fermenting fruits (F) are mostly utilized by domestics or subdomestics of the *melanogaster* and *immigrans* groups, though two wild species of the *melanogaster* group, *D. auraria* and *D. bauraria*, depend mainly on them and some members of the *quinaria* group use them in a subsidiary way. In Europe *D. subobscura* (BEGON, 1975), and in North America *D. affinis* of the *obscura* group, and *D. tripunctata* of the *tripunctata* group, and some others (CARSON and STALKER, 1951) are known to breed on fruits. In

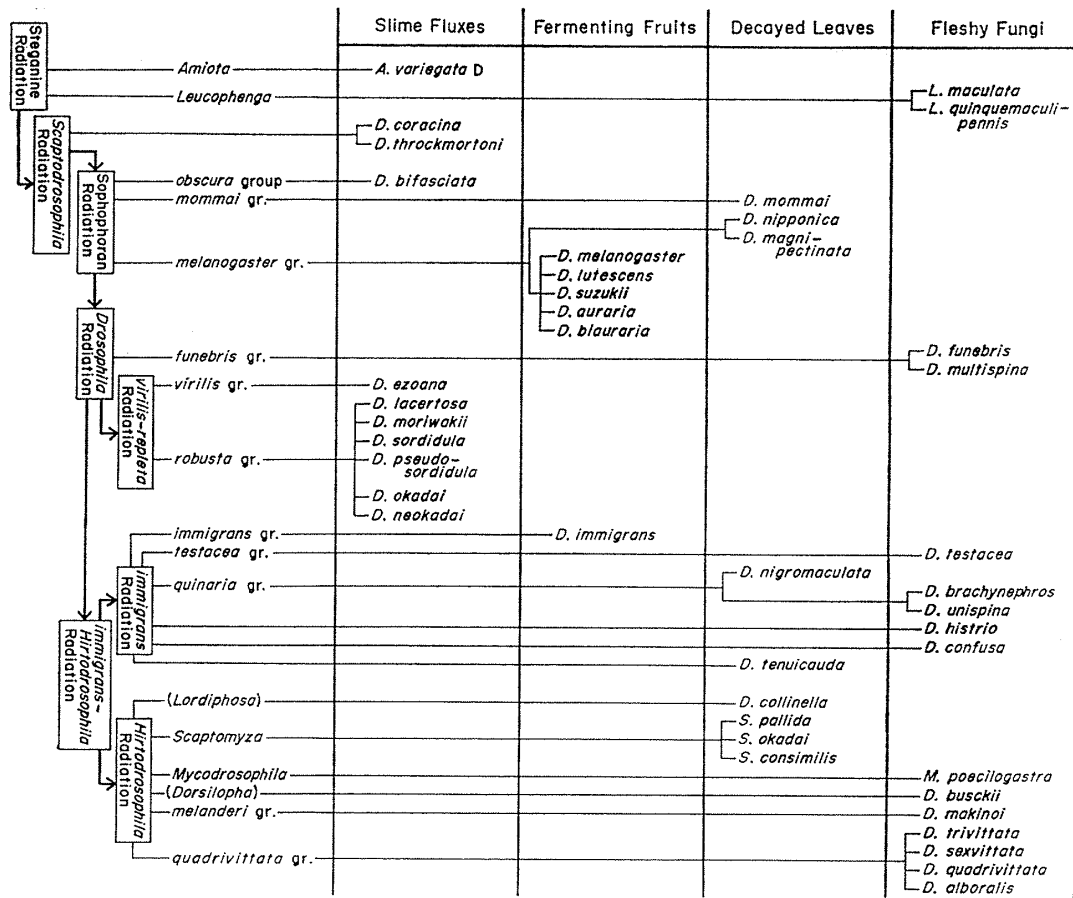


Fig. 1. Phylogenetic relationship of drosophilid flies and their main breeding sites in Hokkaido.

addition to these four types of breeding sites, fresh leaves are known to be utilized by some leaf miners of *Scaptomyza* and *Hirtodrosophila* in temperate regions (FROST, 1924; OKADA, 1968), but this habit was not observed in the present survey.

At the level of the radiation offered by THROCKMORTON (1975), the temperate elements of each radiation show adaptive radiation to two or three types of breeding sites. From the side of breeding sites, a particular site is utilized by separate phyletic lines together: M by four lines, F by two, T by four, and L<sub>1</sub> by three. It is assumed that each line has developed its breeding habit in relation to food resource competition with other members of the sympatric assemblage, though fundamentally based upon its genetic property, and drosophilid flies as a whole may be rather versatile in their breeding habits. The relationship between phylogeny and breeding habits was mentioned for the Hawaiian drosophilid flies by HEED (1968, 1971). He observed that the taxonomically distinct groups showed a similar adaptive radiation for their breeding habits. CARSON (1974) also observed that three species each belonging to distinct phyletic lines innovate



similar niches, breeding on land crabs, assuming this to be as a parallel evolution, accomplished without special genetic conformation.

### Summary

The breeding sites of drosophilid flies were studied in and near Sapporo. Four types of substrates, fermenting fruits, slime fluxes, decayed leaves, and fleshy fungi, were utilized as breeding sites by the 42 drosophilid species. Each species utilized several species of plants, but mainly depended on only one type of substrate. The breeding habits were discussed in relation to phylogeny. At the level of the species group or subgenus the habits were rather uniform, while at the level of the radiation by THROCKMORTON (1975) each radiation was adapted to two or three types of breeding site. The habits of fungus-breeders were compared and two groups were distinguished; the species showing narrow preferences for restricted fungus orders or families, and the species using a wide variety of fungi in a similar manner. The different feeding habits between adults and larvae were observed in the members of the *robusta* and *quinaria* groups and in some others.

### Appendices

**Appendix I.** Plant species utilized for breeding, together with those on which only adults were collected; the former shown in asterisks.

#### Slime fluxes (T)

T1\*) *Ulmus davidiana* var. *japonica*, T2\*) *Ul. laciniata*, T3\*) *Zelkova serrata*, T4\*) *Betula ermanii*, T5\*) *Be. maximowicziana*, T6\*) *Be. platyphylla* var. *japonica*, T7\*) *Fraxinus mandshurica* var. *japonica*, T8\*) *Hydrangea petiolaris*, T9) *Acer mono*, T10) *Cornus controversa*, T11) *Abies sachalinensis*, T12) *Picea jezoensis*, T13\*) Unidentified (wounded plant roots), T14\*) Unidentified (logs of timberyards)

#### Fermenting fruits and hulls (F)

F1\*) *Juglans ailanthifolia*, F2\*) *Morus bombycis*, F3\*) *Prunus mume*, F4\*) *Pr. pauciflora*, F5) *Sorbus commixta*, F6\*) *Actinidia arguta*, F7\*) *Elaeagnus umbellata*, F8\*) *Cornus controversa*, F9\*) *Lilium cordatum* var. *glehnii*, F10\*) *Taxus cuspidata*

#### Decayed leaves (L)

##### Type L<sub>1</sub>

L1\*) *Rumex obtusifolius*, L2\*) *Adonis amurensis*, L3\*) *Anemone flaccida*, L4\*) *Caltha palustris* var. *barthei*, L5\*) *Trifolium repens*, L6\*) *Anthriscus sylvestris*, L7\*) *Cryptotaenia japonica*, L8\*) *Heracleum dulce*, L9\*) *Osmorhiza aristata*, L10\*) *Aralia cordata*, L11\*) *Cirsium kamtschaticum*, L12\*) *Petasites japonicus* var. *giganteus*, L13\*) *Lilium cordatum* var. *glehnii*, L14\*) *Maianthemum dilatatum*, L15\*) *Polygonatum odoratum* var. *maximowiczii*, L16\*) *Smilacina japonica*, L17\*) *Trillium smallii*, L18\*) *Poa pratensis*

##### Type L<sub>2</sub>

L19\*) Unidentified

#### Fleshy fungi (M)

M1\*) *Clitocybe* sp., M2) *Cl. infundibuliformis*, M3\*) *Tricholomopsis decora*, M4\*) *Tr. platyphylla*, M5\*) *Collybia* sp., M6\*) *Co. dryophila*, M7\*) *Co. peronata*, M8\*) *Co. erythropus*, M9\*) *Co. acervata*, M10\*) *Armillariella mellea*, M11\*) *Tricholoma irinum*, M12) *Hohenbuehelia serotina*, M13\*) *Leucopaxillus giganteus*, M14\*) *Pleurotus ostreatus*, M15\*) *Pl. cornucopiae*, M16\*)

*Oudemansiella radicata*, M17\*) *Ou. mucida*, M18) *Flammulnia velutipes*, M19\*) *Mycena haematopus*, M20\*) *My. pura*, M21\*) *My. polygramma*, M22) *My. epipterygia*, M23) *My. sp.*, M24\*) *Lentinellus ursinus*, M25) *Camarophyllus virgineus*, M26\*) *Amanita pantherina*, M27\*) *Am. vaginata*, M28) *Am. sprete*, M29\*) *Pluteus cervinus*, M30) *Plu. leoninus*, M31\*) *Plu. nanus*, M32) *Plu. phlebophorus*, M33\*) *Plu. sp.*, M34) *Agaricus arvensis*, M35\*) *Ag. placomyces*, M36\*) *Ag. sp.*, M37) *Lepiota sp.*, M38) *Le. helveola*, M39) *Le. cygnea*, M40) *Le. subamanitiformis*, M41\*) *Coprinus atramentarius*, M42\*) *Cop. micaceus*, M43) *Cop. disseminatus*, M44\*) *Psathyrella candolleana*, M45\*) *Ps. hydrophila*, M46\*) *Ps. sp.*, M47\*) *Crepidotus mollis*, M48\*) *Cr. sp.*, M49\*) *Naematoloma fasciculare*, M50\*) *Pholiota squarrosa*, M51) *Gymnopilus spectabilis*, M52) *Inocybe sp.*, M53\*) *Rhodophyllus rhodopoliis*, M54\*) *Rh. abortivus*, M55\*) *Russula cyanoxantha*, M56\*) *Ru. emetica*, M57\*) *Ru. nigricans*, M58\*) *Ru. sp.*, M59\*) *Suillus luteus*, M60\*) *Xerocomus badius*, M61\*) *Boletus pulverulentus*, M62\*) *Creolophus spathulatus*, M63\*) *Cantharellus floccosus*, M64) *Polyporellus elegans*, M65\*) *Po. picipes*, M66\*) *Po. squamosus*, M67) *Favolus arcularius*, M68\*) *Fa. alveolarius*, M69\*) *Coriolus bififormis*, M70\*) *Cor. pubescens*, M71\*) *Laetiporus sulphureus* var. *miniatus*, M72) *Fomitopsis insularis*, M73\*) *Tyromyces spumeus*, M74\*) *Sparassis crispa*, M75\*) *Phaeolus schweinitzii*, M76) *Lycoperdon pyriforme*, M77) *Phallus costatus*

**Appendix II.** Plant species utilized by each species, shown with symbols given in Appendix I.

Gothic: utilized for breeding, (n/m): reared numbers of ♀/♂.

*Amiota variegata* D type: T1, T4, T5, T6, T9, T14(0/1), M54

*Leucophenga maculata*: T10, M15, M42, M47, M66(10/4), M68(27/15)

*L. quinque maculipennis*: T5(1/0), M42, M65(2/3), M66(10/10), M73(25/13), M74(0/1)

*Drosophila coracina*: T1, T2(2/3), T3, T4(14/14), T5(6/6), T7, T8, T10, T13(3/4), M10, M14, M26, M42, M44, M65, M66, M71

*D. throckmortoni*: T1(0/1)

*D. bifasciata*: T1, T3(5/3), T4(338/341), T5(155/106), T6(0/2), T8(0/1), T9, T11, T13(70/53), T14(3/3), F3, M54(1/0), M66

*D. mommai*: L2(1/1), L3(1/0), L7(2/1), L17(1/0), M10, M54

*D. nipponica*: T10, F2, L3(7/3), L6(23/10), L8(6/2), L9(21/13), L13(7/4), L14(2/0), L16(2/2), L17(5/4), M10, M41, M44, M56

*D. magnipectinata*: F5, L2(9/3), L3(13/17), L4(1/0), L6(1/0), L8(1/0), L10(2/4), L13(11/6), L14(2/1), L16(2/4), L17(87/88), M10, M17, M54

*D. auraria*: T10, F1(36/34), F2(47/44), F3, F4(28/17), F7, F9(2/5), L3(12/22), M10, M41, M42, M56(1/1), M66

*D. biauraria*: F1(4/2), F2, F3, F4(7/2), F6(5/2), F8(1/1), M10, M24, M35(1/0), M42

*D. lutescens*: F3(0/1), F8(1/9), M42

*D. suzukii*: F2, F3, F7(1/0), F10(9/6), M42, M54, M76

*D. melanogaster*: F3(7/4), F6(42/13), M10(1/0)

*D. funebris*: M7(1/0), M66(2/4)

*D. multispina*: M15, M30, M42(82/68), M66(7/2)

*D. ezoana*: T4(1/1), T5, T12, T14(5/6)

*D. lacertosa*: T5, T7(10/5), T13(39/34), M10, M14, M44

*D. moriwakii*: T2(1/0), T3, T4(5/4), T5(72/110), T6, T7, T8(1/2), T9, T10, T13(301/245)

*D. sordidula*: T1, T4(1/1)

*D. pseudosordidula*: T1(1/2), T2, T4(4/4), T5(5/1)

*D. okadai*: T2, T4, T5, T9, T14(2/3), L19(2/0), M10, M17

*D. neokadai*: T13(1/0), L19(3/0), M44

*D. immigrans*: T1, F1(181/135), F2, F3(1/2), F6(2/5), F9(0/1), L5(1/0), M10(13/15), M17, M34, M41, M42(1/1), M57, M65, M66

*D. testacea*: T1, T2(3/1), T4(3/1), T5(41/30), T9, T10, T13(11/8), F2, F3, L3(15/17), L6(4/8),

- L8(2/6), L12(0/1), L13(25/27), M1, M4(0/1), M6, M7, M9(2/2), M10(5/3), M14(71/71), M15(10/5), M17, M21(2/1), M22, M24(4/0), M25, M26(14/17), M27(0/2), M29(25/9), M31(1/0), M33, M34, M35(5/3), M41(4/5), M42(16/14), M43, M44, M45(3/1), M46(7/7), M47(0/1), M48, M53, M54(1/1), M56(12/9), M57(15/14), M58(18/14), M59(6/1), M60(5/9), M61(5/7), M62, M63(8/8), M65, M66(1/4), M68, M70(3/3), M71
- D. nigromaculata*: T5, T7, T9, T10, F1(5/2), F2(6/3), F4(1/0), F6(5/4), F7, F8(0/2), F9(1/0), L3(55/56), L6(54/55), L8(43/42), L9(2/3), L10(1/0), L12(18/16), L13(25/27), L14(0/1), L15(1/1), L16(1/1), L17(35/27), M4, M10, M14, M19, M23, M24(0/1), M29, M41(7/9), M42(4/8), M43, M44(0/1), M45(1/1), M54, M56, M65, M66(1/4)
- D. brachynephros*: T7, T10, F1(0/3), F6, L6(2/3), L12(0/1), M1(0/1), M4, M6(0/1), M7(2/0), M10(6/4), M14(14/10), M15(12/13), M16(3/2), M18, M19, M20(10/6), M21(15/14), M23, M24(4/0), M25, M26(9/7), M27(2/5), M29(36/36), M30, M31, M33(4/5), M34, M36(6/10), M40, M41(11/12), M42(69/43), M43, M44(16/16), M45(1/0), M46(11/8), M47(1/0), M48(1/2), M50(5/4), M53(3/0), M54, M56(9/10), M57, M59(6/2), M60(4/7), M65, M66, M68, M74, M75
- D. unispina*: F5, F6, L12(0/1), M1(1/0), M4, M5(0/1), M6, M7, M8(8/5), M9(16/13), M10(15/20), M12, M14(2/1), M15(2/1), M17, M19, M20(2/5), M21(16/13), M24, M25, M26(27/47), M27, M29(22/20), M31(3/3), M34, M36(11/20), M37, M38, M41, M42(4/2), M43, M44(2/11), M45(1/1), M46(2/0), M47, M48(6/1), M52, M53, M54, M55(1/0), M56, M57, M58(1/3), M59(1/0), M66, M68, M69(1/1), M70, M76
- D. histrio*: T9, F6, M8(2/0), M9(1/0), M10, M14(1/1), M15(1/0), M17, M26(18/25), M29(0/4), M41(5/5), M42, M44, M45, M54, M56, M66(4/3)
- D. confusa*: T2, T3, T5(0/1), T7, T13(1/2), M1(1/0), M8(1/1), M10(49/47), M13, M14(9/8), M15(122/101), M17, M26(39/35), M27(1/0), M29(14/9), M41(1/0), M42(15/11), M43, M44, M47, M51, M54, M56(7/8), M58(1/0), M60(3/1), M61, M62(5/4), M65(2/6), M66(194/147), M68(0/1), M70(1/0), M71(0/1), M73, M77
- D. tenuicauda*: L3(6/6), L7(6/11), L10(19/9), L13(2/3), M16(4/6), L17(25/22), M21, M54, M62
- Scaptomyza pallida*: T10, F2, F4(1/0), L1(5/8), L3(187/141), L5(57/63), L6(50/38), L8(32/41), L9(22/23), L11(1/0), L12(28/21), L13(8/7), M29, M41, M42, M45(1/0), M69(1/0)
- S. consimilis*: T10, L3(5/3), L4(1/0), L8(0/1), L13(2/0), L17(3/1), M15(1/0), M41, M42
- S. okadai*: L3(0/1), L6(1/0), L8(1/0), L9(1/1), L12(2/1), M75
- Mycodrosophila poecilogastra*: M3, M4, M5(3/9), M10, M14(3/3), M15, M17, M24, M42, M54, M62, M65, M66, M72, M73(0/1), M75(0/4)
- M. japonica*: M4, M10, M14, M24, M42, M47, M65, M66
- M. takachihonis*: M10, M14, M17, M62, M65, M73
- M. shikokuana*: M4, M10, M12, M15, M24, M42, M62, M68, M71, M73
- D. collinella*: T10, L2(15/11), L3(2/9), L6(2/1), L7(5/2), L12(0/2), L13(10/8), L14(1/1), L16(3/0), L17(20/7), M10, M13, M14, M21, M25, M38, M42, M71, M75
- D. busckii*: L1(1/3), L18(1/2), M9(4/0), M10(11/4), M66(17/12)
- D. makinoi*: M4(6/2), M10(0/1), M42, M54(3/4)
- D. quadrivittata*: M10, M13, M14(3/3), M24, M54, M62(1/0), M65(26/24), M66(2/0), M73, M75
- D. trivittata*: M3(0/2), M4(12/12), M8(11/3), M9(2/2), M10(50/25), M13(1/0), M14(179/166), M15(26/20), M17(26/16), M18, M21, M51, M54(0/1), M62, M66
- D. sexvittata*: T9, F1, L10(1/0), M1, M2, M3(0/3), M4(36/26), M5(0/4), M6, M8(10/9), M9(7/11), M10(294/214), M13, M14, M15(6/4), M16(26/42), M17(22/16), M19(2/6), M20, M21, M22, M24, M26(16/13), M27, M29(5/1), M30, M31, M32, M33, M36(3/0), M37, M40, M41, M42, M43, M44(14/11), M45(0/1), M46(0/1), M47(3/0), M48(1/2), M50(28/16), M51, M53, M54(1/0), M55, M56(0/1), M62, M65, M66(8/2), M67, M68, M71, M73, M75

*D. alboralis*: T5, T13(1/0), M1, M2, M3, M4(3/11), M6, M8(8/6), M9(16/13), M10(57/45), M11(1/0), M12, M14(4/2), M15(3/2), M17(16/11), M19, M21(1/0), M22, M24, M26(0/3), M29(23/18), M31(1/0), M35, M37, M41(3/2), M42(5/5), M43, M44(9/7), M45, M47(6/7), M49(3/4), M50(18/21), M54(0/1), M56(0/1), M61, M62, M64, M65(15/11), M66(1/3), M68(1/0), M69(1/0), M70(0/1), M71, M72, M73

### References

- BASDEN, E. B., 1954. The distribution and biology of Drosophilidae (Diptera) in Scotland, including a new species of *Drosophila*. *Trans. R. Soc. Edinb.*, **62**: 603–654.
- BEGON, M., 1975. The relationships of *Drosophila obscura* FALLÉN and *D. subobscura* COLLIN to naturally-occurring fruits. *Oecologia*, **20**: 255–277.
- BEPPU, K., A. KANEKO, M. J. TODA, and M. T. KIMURA, 1977. Methods in the studies of wild drosophilid flies in Hokkaido. 2. Key to species of Drosophilidae in Hokkaido, with a supplementary note on phylogeny. *Seibutsu Kyozaï*, **12**: 1–40. (In Japanese.)
- BURLA, H. and G. BÄCHLI, 1968. Beitrag zur Kenntnis der schweizerischen Dipteren, insbesondere *Drosophila*-Arten, die sich in Fruchtkörpern von Hutpilzen entwickeln. *Vierteljahrsschrift Naturf. Ges. Zürich*, **113**: 311–336.
- CARSON, H. L., 1951. Breeding sites of *D. pseudoobscura* and *D. persimilis* in the transition zone of the Sierra Nevada. *Evolution*, **5**: 91–96.
- 1971. The ecology of *Drosophila* breeding sites. Harold L. Lyon Arboretum Lecture Number **2**: 1–27.
- 1974. Three flies and three islands: Parallel evolution in *Drosophila*. *Proc. Nat. Acad. Sci. USA*, **71**: 3517–3521.
- , E. P. KNAPP and H. J. PHAFF, 1956. Studies on the ecology of *Drosophila* in the Yosemite region of California. III. The yeast flora of the natural breeding sites of some species of *Drosophila*. *Ecology*, **37**: 538–544.
- , and H. D. STALKER, 1951. Natural breeding sites for some wild species of *Drosophila* in the eastern United States. *Ibid.*, **32**: 317–330.
- FROST, S. W., 1924. A study of the leaf mining of Diptera of North America. *Cornell Agric. Exp. Sta. Memoir*, **78**: 1–228. (Not directly accessible.)
- HEED, W. B., 1968. Ecology of the Hawaiian Drosophilidae. *Univ. Texas Publ.*, **6818**: 387–419.
- 1971. Host plant specificity and speciation in Hawaiian *Drosophila*. *Taxon*, **20**: 115–121.
- HERTING, B., 1955. Untersuchungen über die Ökologie der wildlebenden *Drosophila*-Arten westfalens. *Z. Morph. u. Ökol. Tiere*, **44**: 1–42.
- KIMURA, M. T., 1976 a. *Drosophila* survey of Hokkaido, XXX. Microdistribution and seasonal fluctuations of drosophilid flies dwelling among the undergrowth plants. *J. Fac. Sci. Hokkaido Univ.*, (VI-Zool) **20**: 192–202.
- 1976 b. *Drosophila* survey of Hokkaido, XXXII. A field survey of fungus preferences of drosophilid flies in Sapporo. *Ibid.*, **20**: 288–298.
- MOMMA, E., 1965. The dynamic aspects of *Drosophila* populations in semi-natural areas. 1. Associations and relative numbers of species. Part 2. Results of sweeping. *Japan. J. Genet.*, **40**: 297–305.
- OKADA, T., 1968. Systematic Study of the Early Stages of Drosophilidae. 188 pp. Bunka Zugsisha Co., Tokyo.
- PIPKIN, S. B., R. L. RODRÍGUEZ and J. LEÓN, 1966. Plant host specificity among flower-feeding neotropical *Drosophila* (Diptera: Drosophilidae). *Am. Nat.*, **100**: 135–156.
- SHORROCKS, B. and A. M. WOOD, 1973. A preliminary note on the fungus feeding species of *Drosophila*. *J. nat. Hist.*, **7**: 551–556.
- SPENCER, W. P., 1942. New species in the *quinaria* group of the subgenus *Drosophila*. *Univ. Texas Publ.*, **4213**: 53–66.
- THROCKMORTON, L. H., 1975. The phylogeny, ecology, and geography of *Drosophila*. In R. C. KING ed. *Handbook of Genetics* **3**: 421–469. Plenum Publ.
- TODA, M. J., 1973. Influence of forest felling upon drosophilid fauna at several localities in Hokkaido. *Res. Bull. Coll. Exper. Forests, Coll. Agr., Hokkaido Univ.*, **30**: 389–410.