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# Evolution of Food Preference in Drosophilidae: An Ecological Approach

By

Masahito T. Kimura

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Contents

# Introduction

The concept of evolution is basic to the life science. The morphological, physiological, or ecological characters of organisms have been evolved in interactions with their environments in the progress of time from the past to the present~~s~~. Dobzhansky <u>et</u> <u>al</u>. (1975) defined organic evolution as " a series of partial or complete and irreversible transformations of the genetic composition of populations, based principally upon altered interactions with their environment." Genetic studies have shown the genetic composition of populations or species, and population genetics has established the theoretical framework for the transformations of the genetic compositions of populations and also for the maintenance of the genetic variations in populations. On the other hand, ecology is the study of the relationships between organisms and their environments, and this study enables us to understand how natural selection operates on organisms and also transforms the genetic composition. The study of population ecology is particularly important for the study of evolution, because natural selection changes the genetic quality of populations through changes of population size. Evolutionary ecology has been trying to explain theoretically the causes and processes of evolution of morphological, physiological, and ecological characteristics on the basis of the concept of natural selection and population ecology (see for reviews, Emlen, 1973; Pianka, 1974; Price, 1975). But examination of the hypotheses which have derived from these theoretical studies is not advanced so far in the real world, because of lack of information on organisms in natural areas.

*Drosophila* species are excellent materials for genetic studies. The chromosomal polymorphisms, particularly inversions of chromosomes, are studied with the giant chromosome of the salivary gland (Dobzhansky and Epling, 1944; Dobzhansky, 1957; Powell *et al.*, 1973; etc.). The frequency of lethals or semilethals has also been surveyed in several natural populations of some *Drosophila* species (Dobzhansky and Spassky, 1954, 1963, 1968; etc.). Hubby and Lewontin (1966), using the technique of gel electrophoresis, elucidated the allelic variation in several enzymic genes in *Drosophila pseudoobscura*. This method is now applied to many animals and plants as well as other *Drosophila* species (see for reviews, Lewontin, 1974; Selander, 1976). These studies elucidated the existence of many genetic variations in populations or species. These genetic variations, however, are not the target of natural selection until they are expressed in morphological or physiological traits which interact directly with environments. At the present time, the expression and adaptive function of these variations are little known, and thus it is not clear how natural selection operates on such genetic variations.

Compared with the enormous ragnge of genetic studies on *Drosophila*, there is still a lack of ecological studies. The food of *Drosophila* species has been studied for a long time. The basic biological role of these flies appears to be that they are primarily consumers of the microoganisms, yeast and bacteria, which are in turn associated with the initial stages of decay of plant materials, such as fruit, flowers, tree saps, barks, leaves, or fleshy fungi (Carson, 1971). Some species are known to feed and breed on fresh or living plant materials,: flowers (Sturtevant, 1921; Brncic, 1966; Pipkin *et al*., 1966), living leaves (Frost, 1924; Okada, 1968), and fruit (Lachaise, 1977). Some species innovate very special feeding habits; breeding on land crabs (Carson, 1974), or spider's eggs (Heed, 1968). Compared with the knowledge on the feeding and breeding habits of *Drosophila* species, ecology of their food plants is only little known, and this obstructs the evolutionary study of their feeding habits.

The habitats or microdistributions of *Drosophila* are rather well known, because much work has centered on this point. Most species prefer forest environments, but some are abundant in open areas. In forests some prefer the streamside (Toda, 1973a; Beppu, 1976), some do the canopy (Basden, 1954; Toda, 1977), and some the undergrowth layer (Toda, 1977). Dobzhansky and Pavan (1950) observed a patchy distribution of flies in a forest in Brazil, and the flies changed the distribution pattern from month to month. The pattern of distribution also varies for different species, which are attracted to different kinds of food. Similar data were obtained in England (Shorrocks, 1970).

The study of their seasonality has been made through analyses of ovarian conditions in natural populations (Lakovaara et al., 1972; Lumme et al., 1974; Begon, 1976; Watabe and Beppu, 1977). According to these papers, most temperate Drosophila species pass winter as adult in the reproductive diapause, and repeat several generations during periods free from diapause. Fluctuations of their population sizes during active periods have been studied extensively (Patterson and Stone, 1952; Herting, 1955; Mather, 1956; Wakahama, 1956, 1957, 1962; Toda, 1973; Lachaise, 1974; etc.). Some studies (Dobzhansky and Epling, 1944; Hunter, 1966) discussed the fluctuations in connection with climatic conditions, and Pipkin (1965) studied the fluctuations of ground-feeding Drosophila in relation to the seasonality of foods in Panama, b~~B~~ut many studies remain~~e~~ descriptive.

Competition of Drosophila has been studied in the laboratory conditions. Sokoloff (1955) studied the larval competition of the American species of the obscura group,

D. pseudoobscura, D. persimilis, and D. miranda, and observed that the interspecific competition is more intense than the intraspecific competition. Ayala (1969, 1970, 1971) studied competitive coexistence of Drosophila species and suggested the possibility that two species coexist under competition through the frequency dependent selection. However, no analytical study has been carried out on competition of Drosophila in natural areas.

The ecological characteristics of drosophilid flies, such as food preferences, habitat preferences, or seasonality, have been evolved in interaction with environmental, climatic, and food conditions. Competition with other species and predation also have deep influence on the evolution of competitive and escape abilities, and also of food preferences or seasonality through the regulation of population increase. But, up to the present, no attempt was made to understand the evolution of such ecological characteristcs of Drosophila species in connection with the ecological factors. In this thesis, the author provides the feeding and breeding preferences, seasonality, and microdistribution of drosophilid species in Hokkaido, and discusses the evolution of food preferences in connection with ecology of their food plants, the competition between species, and seasonality of the flies. In addition, the seasonal fluctuation and microdistribution are discussed on the basis of the seasonal life cycles, feeding and breeding habits, and habitat preferences of the flies.

# PART I

# Breeding and Feeding Sites of Drosophilid Flies in and near Sapporo, Northern Japan

# Introduction

Life can not survive and reproduce without energy. Then, a study of food preference is essential for ecological study of animals. Reviewing previous contributions, Carson (1971) classified the various breeding substrates of larvae of *Drosophila* 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 r~~i~~egions (Frost, 1924; Carson and Stalker, 1951; Okada, 1968 ; etc.). In Hokkaido, only fragmentary records of the breeding sites of drosophilid flies are known. Adult flies generally feed on materials for breeding, but some works (Carson *et al.*, 1956; Pipkin, 1965; Heed, 1968) have emphasized observations which indicate that there is often a clear separation of adult and larval foods. This part reports the breeding and feeding sites of drosophilid flies confirmed through surveys carried out in and near Sapporo, together with discussion on the relationships between the phylogeny and breeding habits of drosophilid flies.

## 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 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. 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 FR, TR, LV, and MS. 1) FR: 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 has terminated. 2) TR: 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 (1973b) 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 is therefore counted as one unit in Table 1. 3) LV: Decayed leaves and stems are divided into $LV_1$ of herbaceous plants (18 species), and $LV_2$ of unidentified arboreal plants which have drifted to river shores. 4) MS: Fourty-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. Table 1 shows numbers of plant species utilized by each species for breeding separately for each type of breeding site, together with records of adult collections. Where the utilized species form 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 relatively 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 conifera takadai* was reared from TR. *Leucophenga maculata* and *L. quinquemaculipennis* were observed breeding on MS.

Table 1. Numbers of plant species utilized by each species for breeding(B), separately present for each type of breeding site, together with records of adult collections(C).

| Types of breeding sites | Slime fluxes | | Fermenting fruits | | Decayed leaves | | | Fleshy fungi | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | $LV_1$ | $LV_2$ | | | |
| | B | C | B | C | B | B | C | B | C |
| Total plant species number | 10 | 12 | 9 | 8 | 18 | 1 | | 55 | 71 |
| Steganine radiation | | | | | | | | | |
| *Amiota conifera takadai* | 1 | 5 | - | - | - | - | - | - | 1 |
| *Leucophenga maculata* | - | 1 | - | - | - | - | - | 2 | 5 |
| *L. quinquemaculipennis* | 1 | - | - | - | - | - | - | 4 | 1 |
| *Scaptodrosophila* radiation | | | | | | | | | |
| *Drosophila coracina* | 4 | 8 | - | - | - | - | - | - | 8 |
| *D. throckmortoni* | 1 | - | - | - | - | - | - | - | - |
| Sophophoran radiation | | | | | | | | | |
| *D. bifasciata* | 7 | 7 | - | 1 | - | - | - | 1 | 1 |
| *D. mommai* | - | - | - | - | 4 | - | + | - | 2 |
| *D. nipponica* | - | 1 | - | 1 | 8 | - | + | - | 4 |
| *D. magnipectinata* | - | - | - | 1 | 10 | - | + | - | 3 |
| *D. auraria* | - | 1 | 4 | 4 | 1 | - | - | 1 | 5 |
| *D. biauraria* | - | - | 4 | 3 | - | - | - | 1 | 3 |
| *D. lutescens* | - | - | 2 | 1 | - | - | - | - | 1 |
| *D. suzukii* | - | - | 2 | 2 | - | - | - | - | 3 |
| *D. melanogaster* | - | - | 2 | - | - | - | - | 1 | - |
| *Drosophila* radiation | | | | | | | | | |
| *D. funebris* | - | - | - | - | - | - | - | 2 | 1 |
| *D. multispina* | - | - | - | - | - | - | - | 2 | 3 |

Table 1. continued

| Type of breeding sites | Slime fluxes | | Fermenting fruits | | Decayed leaves $LV_1$ | $LV_2$ | | Fleshy fungi | |
|---|---|---|---|---|---|---|---|---|---|
| | B | C | B | C | B | B | C | B | C |
| *virilis-repleta* Radiation | | | | | | | | | |
| *D. ezoana* | 2 | 3 | - | - | - | - | - | - | - |
| *D. lacertosa* | 2 | 2 | - | - | - | - | - | - | 3 |
| *D. moriwakii* | 5 | 8 | - | - | - | - | - | - | 2 |
| *D. sordidula* | 1 | 1 | - | - | - | - | - | - | - |
| *D. psudosordidula* | 3 | 3 | - | - | - | - | - | - | - |
| *D. okadai* | 1 | 4 | - | - | - | 1 | - | - | 2 |
| *D. neokadai* | 1 | - | - | - | - | 1 | - | - | 1 |
| *immigrans* Radiation | | | | | | | | | |
| *D. immigrans* | - | 1 | 4 | 3 | 1 | - | - | 2 | 8 |
| *D. testacea* | 4 | 6 | - | 2 | 5 | - | - | 27 | 40 |
| *D. nigromaculata* | - | 4 | 6 | 5 | 11 | - | + | 6 | 16 |
| *D. brachynephros* | - | 2 | 1 | 1 | 2 | - | - | 27 | 39 |
| *D. unispina* | - | - | - | 2 | 1 | - | - | 22 | 40 |
| *D. histrio* | - | 1 | - | 1 | - | - | - | 8 | 11 |
| *D. confusa* | 2 | 4 | - | - | - | - | - | 19 | 22 |
| *D. tenuicauda* | - | - | - | - | 6 | - | + | - | 3 |
| *Hirtodrosophila* Radiation | | | | | | | | | |
| *Scaptomyza pallida* | - | 1 | 1 | 2 | 9 | - | + | 2 | 3 |
| *S. consimilis* | - | 1 | - | - | 5 | - | + | 1 | 2 |
| *S. okadai* | - | - | - | - | 5 | - | + | - | 1 |
| *Mycodrosophila poecilogastra* | - | - | - | - | - | - | - | 4 | 15 |
| *D. collinella* | - | 1 | - | - | 9 | - | + | - | 9 |
| *D. busckii* | - | - | - | - | 2 | - | - | 3 | - |
| *D. makinoi* | - | - | - | - | - | - | - | 3 | 4 |
| *D. trivittata* | - | - | - | - | - | - | - | 10 | 13 |
| *D. sexvittata* | - | 1 | - | 1 | 1 | - | - | 22 | 47 |
| *D. quadrivittata* | - | - | - | - | - | - | - | 4 | 10 |
| *D. alboralis* | 1 | 1 | - | - | - | - | - | 25 | 38 |

The *Scaptodrosophila* radiation: *Drosophila coracina* and *D. throckmortoni* were reared from TR.

The Sophophoran radiation: *Drosophila bifasciata* of the *obscura* group utilized TR as the main breeding site, including one specimen reared from MS. One species of the *mommai* group, *D. mommai*, bred on LV$_1$. 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 LV$_1$, 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 *funebris* group, *D. funebris* and *D. multispina*, bred on MS.

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 TR. It is noteworthy that the last two species were observed breeding on the decayed leaves and stems which had drifted on river shores (LV$_2$).

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 FR, *D. nigromaculata* for LV$_1$, and *D. testacea* for MS. *Drosophila brachynephros*, *D. unispina*, *D. histrio*, and *D. confusa* bred on MS in the main, and *D. tenuicauda* on $LV_1$.

The *Hirtodrosophila* radiation: Three species of *Scaptomyza*, *S. pallida*, *S. consimilis*, and *S. okadai*, were confirmed mainly breeding on $LV_1$, though the first two also bred, but seldom, on MS or FR. *Mycodrosophila poecilogastra* was observed breeding on MS. The members of the *quadrivittata* group, *D. quadrivittata*, *D. trivittata*, *D. sexvittata*, and *D. alboralis*, also utilized MS as the main breeding site. In addition to MS, *D. sexvittata* was reared from $LV_1$, and *D. alboralis* from TR. *Drosophila collinella* of the subgenus *Lordiphosa* bred on $LV_1$, *D. busckii* of the subgenus *Dorsilopha* on MS and $LV_1$, and *D. makinoi* of the *melanderi* group on MS.

It was frequently observed that several species of drosophilid flies bred on the same species of plant or fungus. Here degree of niche overlap of these drosophilid species is measured in following formula:

$$d_{ij} = \frac{a_{ij}}{n_i+n_j}$$

where $d_{ij}$ is degree of niche overlap between species i and j, $n_i$ and $n_j$ are number of plant and fungus species used for breeding by species i and j respectively, and $a_{ij}$ is number of plant and fungus species used for breeding by both of species i and j. Fig. 1 shows the result of clustering (the unweighted variable group method,

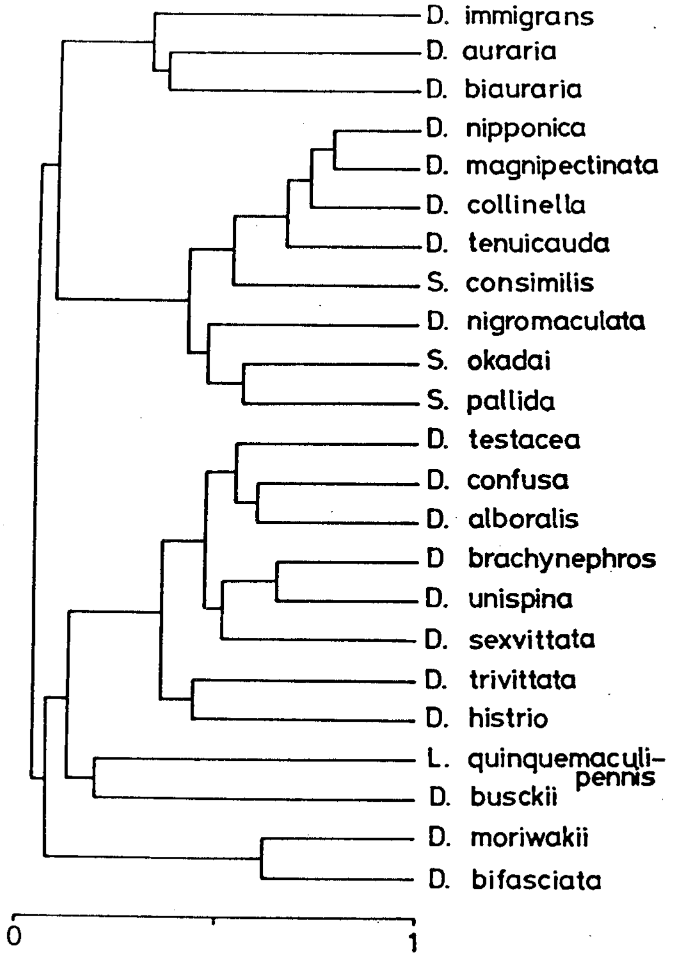

Fig. 1. Dendrogram resulting from the cluster analysis based on the survey of breeding sites.

Sokal and Sneath, 1963) based on the degree of niche overlap. The analysis was made for species which were observed breeding on more than 5 species of plants or fungi. The drosophilid association in and near Sapporo was divided into four, fruit feeders, herbage feeders, fungus feeders, and sap feeders.

## 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 the decayed leaves ($LV_1$), 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 for adult feeding by D. coracina, D. collinella, and some members of the melanogaster and robusta groups. Carson and Stalker (1951) also observed that adults of D. robusta fed but not oviposited 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 (Part II), 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 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, most species mainly depend on only one breeding site among the four types. In several cases, even species widely using three types select one type as the main breeding site, e.g., *D. auraria* and *D. immigrans* mainly for FR, *D. brachynephros* and *D. testacea* for MS, and *S. pallida* and *D. nigromaculata* for $LV_1$. On the other hand, the plant host specificity of the fly species concerned in the present study is not so rigid as 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.

Fig. 2 illustrates the relationship between the breeding habits and phylogeny of species offered by Throckmorton (1975). These four breeding sites are

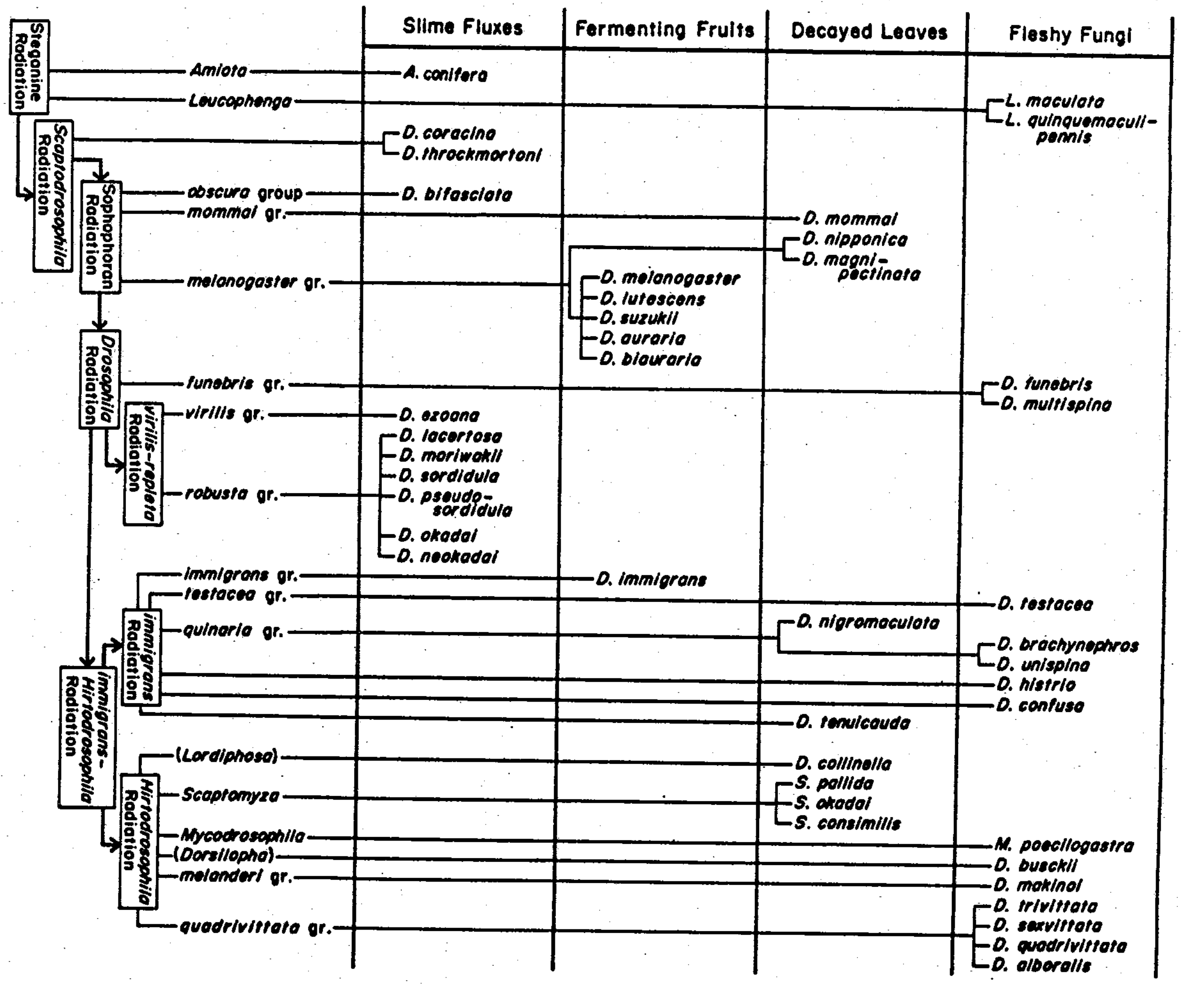

Fig. 2. Phylogenic relationship of drosophilid flies and their main breeding sites in Hokkaido.

also utilized by drosophilid flies in other parts of the world, but associated members of each site are not the same. Then the comparison of associated members among localities would give information on evolution of drosophilid community and their feeding habits.

Slime fluxes were used chiefly by members of *Scaptodrosophila*, the *obscura*, *robusta*, and *virilis* groups in Hokkaido. In other temperate regions, North America and Europe, the same groups are known as sap feeders, though Europe lacks the *robusta* group (Gordon, 1942; Carson, 1950; Carson and Stalker, 1951; Basden, 1954). In tropical regions only the members of *Scaptodrosophila* are known as sap feeders, but this subgenus has many species there (Burla, 1954; Lachaise, 1974). These sap feeders are generally restricted to forests perhaps by their feeding habits (Toda, 1973a; Kimura and Toda, 1976; Beppu, 1976, 1978), and usually have black bodies (Okada, 1962).

Most of fruit feeders in Hokkaido are domestic or subdomestic species; *D. immigrans* and *D. melanogaster* are known as the famous domestic species and *D. suzukii*, *D. lutescens*, and *D. auraria* are found mainly in human habitations or artificially disturbed areas in Hokkaido (Kaneko and Tokumitsu, 1963; Toda, 1973a; Watabe, in press), though they are found in natural areas in southern Japan. Only *D. biauraria* is wild species in Hokkaido. It would be due to the facts that the natural fruits are rare in Hokkaido, and the fruiting season is usually after their breeding season has terminated. In other temperate regions, this site is also not used by specialized fruit feeders; by *D. subobscura* of the *obscura* group in England (Begon, 1975) and by *D. affinis* of the *obscura* group and *D. tripunctata* of the *tripunctata* group in North America (Carson and Stalker, 1951). Fruits, therefore, are not a stable breeding site for temperate drosophilid flies. In tropics where natural fruits are abundant, however, this site ~~is~~ occup~~ied~~y an important situation; it is used by several major groups, the *immigrans* and *melanogaster* groups in the Palaeotropical region, and the *willistoni* and *tripunctata* groups in the Neotropical region. These groups have bursts of species in tropical areas (Burla, 1954; Magalhaes, 1962; Wheeler and Magalhaes, 1962; Bock and Wheeler, 1972).

Decayed leaves and stalks of herbaceous plants, which hitherto have not been reported as breeding sites in the continental areas, are utilized by some members of the Sophophoran radiation and the *immigrans-Hirtodrosophila* radiation. In the Sophophoran radiation, *D. nipponica* and *D. magnipectinata* of the *melanogaster* group and *D. mommai* of the *mommai* group breed mainly on these substrates. As discussed previously, the members of the *melanogaster* group are usually fruit feeders, and abundant in tropical areas. The successful invasion of *D. nipponica* and *D. magnipectinata* to the temperate region would be supported partly by their characteristic breeding habits. In the *immigrans*-*Hirtodrosophila* radiation various species utilized this site mainly or subsidiarily. *Drosophila nigromaculata* of the *quinaria* group is one of the most dominant herbage feeder in Hokkaido. *D. palustris* which is closely related species of *D. nigromaculata* also breeds on decayed water plant in North America (Spencer, 1942). Several species of the *Scaptomyza* breed on decayed leaves. Up to the present, species of this genus are known as leaf-miner (Frost, 1924; Okada, 1968; Basden, 1971; Nishiharu, 1978). As the basic feeding or breeding habit of Drosophilidae is saprophagous, the leaf-mining habit of these species would have ~~be~~ evolved from the saprophagic herbage feeding habit. A species of *Lordiphosa*, *D. collinella*, uses also this site, and two Europ~~i~~ean species of this subgenus, *D. fenestrarum* and *D. andalusiaca*, may breed on decayed leaves, because they are collected exclusively by net sweeping on herbaceous plants (Herting, 1955). In Hawaii, a considerable number of species breed on fermenting leaves, and most of them are monophagous (Heed, 1968). But the herbage feeders of Hokkaido usually use several families of plants.

Fleshy fungi were utilized by three radiation in Hokkaido, the Steganine, *Drosophila*, and *immigrans*-*Hirtodrosophila* radiations. Europe and North America also have similar fauna of fungus feeders. The Paleotropic region has ~~a~~ many species of *Hirtodrosophila* and *Mycodrosophila* (Burla, 1954; Okada, 1967; Bächli, 1973), and the Neotropical region has a considerable number of species of *Zygothrica*, a related genus of *Hirtodrosophila*, (Throckmorton, 1975). The ecology and breeding habits of these tropical species are little known.

Besides these substrates, living flowers or land crabs are used by several species in tropical regions (Pipkin *et al.*, 1966; Carson, 1971, 1974), but not known in the temperate regions.

As referred above, one breeding site was used by several different groups. These groups perhaps evolved their breeding habits independently, and it suggests the parallel evolution of feeding habit or preference. Heed (1971) also observed that the taxonomically distinct groups of Hawaiian *Drosophila* showed a similar adaptive radiation for their breeding habits. Carson (1974) reported that three species each belonging to distinct phyletic lines innovate similar niches, breeding on land crabs, assuming this to be as a parallel evolution.

The considerable overlap of food niche was observed among the species dwelling in Sapporo. How they coexist sympatrically is not known at present. In the later parts, detail study of food preference will be reported for fungus feeders and their coexistence will be discussed

# PART II

## Evolution of Food Preference in Fungus Feeding *Drosophila*

# Introduction

Evolution of food preference of insects has received, much attention for a long time. But it is difficult to trace the course of the evolution from a species to others, partly because each species already has a distinct preference, and there are little known the successive transformations of food preference. Insufficient knowledges on physiological mechanism and genetics of food preference also prevent the study of its evolution. Emlen (1973) and Pianka (1974) provided theoretical frameworks on the evolution and determination of food preferences in relation to the "value" of food, which is determined by food quality and abundance. But examination of the theory did not proceed so far, because there have been only few studies of food preferences in relation to ecology of host plants. In *Drosophila*, evolution of food preferences was studied on neotropical flower-feeders by Pipkin *et al*. (1966), on *D*. *pachea* which breeds on a senita cactus by Heed and Kircher (1965), and on some crab flies by Carson (1974). These species use new types of food aparting from the original saprophagous habits of this genus. However, the cause of evolution of food preferences in these flies was not known. Here the author reports the food preference of adults and larvae of fungus-feeding species of the *immigrans*-*Hirtodrosophila* radiation, and discusses on the process and cause of evolution of food preference.

## Methods

### Field observation

Fungus preferences of species for breeding are studied examining the results of Part I. Further, to know which parts of fungi, pileus or stipe, larvae feed on, individuals emerged from these parts were collected separately.

To study fungus preferences of adult flies, periodical collections of adult flies from naturally occurring fleshy fungi were carried out at four localities in Hokkaido, the Botanical Garden of Hokkaido University, the Nopporo Natural Forest, the Moiwa Natural Forest, and the Nakagawa Experimental Forest of Hokkaido University. The first three are located in or near Sapporo, and the natural vegetation is deciduous broad leaved forest admixed with some conifers. The last is located in northern Hokkaido, and composed mainly of coniferous trees. In the Botanical Garden, the collections were made for eight days in the end of May and in the beginning of each month from June to October in 1973, and for four days at each collecting period in the beginning and middle of each month from May to October in 1974. The collecting area which consists of five stations is about 7500 $m^2$ on the floor of groves in total. At the Nopporo Natural Forest and the Moiwa Natural Forest, the collections were made for two days at each collecting period in the beginning and middle of each month from June to October in 1975. The collections were performed along paths or streams, 900 m in the Moiwa (consisting of two stations) and 1,100 m in the Nopporo (consisting of three stations). At the Nakagawa Experimental Forest the collections were made along paths (3,000 m) for two days in the middle of each month from June to October in 1973. The flies were collected from all of fleshy fungi which were found in the collecting areas or along paths three times a day, at 13:00, 15:00, and 17:00 hours. At the same time most fleshy fungi were identified and counted, but some species difficult to identify were collected for accurate identification.

In order to study on the successive change of the drosophilid fauna in relation to the decay of fungi, flies were collected from several kinds of fungi every day except rainy days from appearance of the fungi to their disappearance by decay in the Botanical Garden. The collections were also made three times a day, at 13:00, 15:00, and 17:00 hours.

### Laboratory experiment

Species used in the experiments are shown in Table 14. These species except for *D. immigrans* and *D. nigromaculata* use fungi as the main breeding site as shown in the Part I. *D. immigrans* is a fruit feeder and *D. nigromaculata* is a herbage feeder. Most specimens used in the experiments are collected in Sapporo and maintained few days on yeast-agar medium. But specimens of *D. alboralis* were $G_1$ offspring of field collected females.

Mortality and egg productivity on different foods: Ten females were maintained on six foods, agar medium (agar 1.4%), yeast-agar medium (agar 1.4%, dry yeast 8%), banana, fresh *Pleurotus cornucopiae*, decayed *P. cornucopiae*, and fresh *Agaricus bisporus*. The fungi used were cultivated ones. Number of dead flies and number of eggs oviposited were counted daily for ten days, and foods were refreshed at the same time.

Preferences of adult flies to fresh and decayed fungi: About 30 females were introduced into the container (1,300 ml) which contained fresh, intermediate, and decayed *Pleurotus cornucopiae* (5 g). The decayed fungi were obtained by leaving fresh fungi for four days to room temperature and the intermediate ones were by leaving for two days to the same condition. The container was kept under feeble light condition at 20±1° C. Number of adults attracted to these fungi was counted 12 times at one hour interval from introduction, and number of eggs oviposited on these fungi was counted after 24 hours. At the same time on which parts of fungi, stipe, upper surface of pileus, or lamella, they oviposited eggs were examined.

Preferences of larvae to fresh and decayed fungi:

The second or third instar larvae which were cultured on the yeast-agar medium were introduced into a Petri dish which contained the fresh, intermediate, and decayed P. cornucopiae (0,5 g) and after three hours number of larvae attracted to these fungi was counted.

Larval viability on yeast medium: Eggs which were sterilized by 70% alcohol were put on the sterilized yeast-agar-sugar medium (agar 1.4%. dry yeast 8%, sugar 5%, propionic acid as antiseptic solution 0.5%), and number of adults emerged was counted.

# Results

## 1. Field observation

### *Fungus preferences for breeding*

Table 2 shows number of species of Aphyllophorales and each family of Agaricales used by the members of the *immigrans-Hirtodrosophila* radiation for breeding. *Drosophila nigromaculata*, a herbage feeder, prefers the fungi of family Coprinaceae. *D. trivittata* has a strong preference for the family Tricholomataceae, and *D. quadrivittata* and *Mycodrosophila poecilogastra* for Tricholomataceae and Aphyllophorales. The remaining species, *D. sexvittata*, *D. alboralis*, *D. confusa*, *D. testacea*, *D. brachynephros*, and *D. unispina*, use a wide range of fungi, but *D. confusa* shows a preference for Aphyllophorales rather than the others. Table 3 gives number of individuals which were reared from fungi of Aphyllophorales and each family of Agaricales. This result supports the preference of *D. confusa* for Aphyllophorales. Though *D. sexvittata* shows a wide preference, it breeds frequently on fungi of Tricholomataceae compared with others.

Table 4 shows number of individuals of each species which were reared from pilei and stipes of three species of fungi, *Oudemansiella mucida*, *Armillariella mellea*, and *Pluteus cervinus*. This clearly shows that *D. trivittata*, *D. sexvittata*, and *D. unispina* breed mainly

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

| Oder | Aphyllophorales | Agaricales | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Family | | Tr | Am | Ag | Co | Cr | St | Rh | Ru | Bo |
| Total species No. | 11 | 19 | 5 | 2 | 5 | 2 | 2 | 2 | 4 | 3 |
| *M. poecilogastra* | 2 | 2 | - | - | - | - | - | - | - | - |
| *D. quadrivittata* | 3 | 1 | - | - | - | - | - | - | - | - |
| *D. trivittata* | - | 9 | - | - | - | - | - | 1 | - | - |
| *D. sexvittata* | 1 | 10 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | - |
| *D. alboralis* | 5 | 9 | 3 | - | 3 | 1 | 2 | 1 | 1 | - |
| *D. confusa* | 6 | 5 | 3 | - | 2 | - | - | - | 2 | 1 |
| *D. testacea* | 3 | 7 | 4 | 1 | 4 | 1 | - | 1 | 3 | 3 |
| *D. brachynephros* | - | 10 | 4 | - | 5 | 2 | 1 | 1 | 1 | 2 |
| *D. unispina* | 1 | 9 | 4 | 1 | 4 | 1 | - | - | 2 | 1 |
| *D. nigromaculata* | 1 | 1 | - | - | 4 | - | - | - | - | - |

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

Table 3. Numbers of individuals of each species reared from fungi of Aphyllophorales and each family of Agaricales

| Oder | Aphyllophorales | Agaricales | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Family | | Tr | Am | Ag | Co | Cr | St | Rh | Ru | Bo |
| D. sexvittata | 10 | 738 | 35 | 3 | 27 | 6 | 44 | 1 | 1 | - |
| D. alboralis | 33 | 199 | 45 | - | 31 | 13 | 46 | 1 | 1 | - |
| D. confusa | 361 | 339 | 98 | - | 27 | - | - | - | 17 | 4 |
| D. testacea | 27 | 187 | 68 | 8 | 57 | 1 | - | 2 | 82 | 33 |
| D. brachynephros | - | 117 | 104 | 16 | 187 | 3 | 9 | 3 | 19 | 17 |
| D. unispina | 2 | 121 | 187 | 31 | 23 | 7 | - | - | 4 | 1 |

Abbreviations for family name, cf. Table 2.

Table 4. Numbers of individuals of each species reared from pilei and stipes of Oudemansiella mucida (Ou), Armillariella mellea (Ar), and Pluteus cervinus (Pu).

| Fungus | Ou | | Ar | | Pu | |
|---|---|---|---|---|---|---|
| | Pileus | Stipe | Pileus | Stipe | Pileus | Stipe |
| D. trivittata | 836 | 15 | 83 | 1 | - | - |
| D. sexvittata | 87 | 7 | 56 | 2 | 13 | 3 |
| D. alboralis | 10 | 86 | 18 | 16 | - | - |
| D. testacea | 2 | 2 | - | - | 26 | 13 |
| D. unispina | - | - | 15 | - | 30 | 1 |

on pileus of fungi, but, D. alboralis and D. testacea breed frequently on stipe.

Fungus preferences of adult flies

Table 5 shows individual numbers of abundant species collected from the main 13 species of fungi in the Botanical Garden for two years. The members of the immigrans radiation, D. nigromaculata, D. brachynephros, D. unispina, and D. testacea, were mostly collected from the fungi of Coprinaceae, though they were collected from other various fungi frequently, and D. confusa was attracted mainly to Coprinus micaceus and Polyporellus squamosus. D. sexvittata preferred P. squamosus, though it was collected from various fungi in good number. D. trivittata was collected exclusively

Table 5. Numbers of individuals of the main species collected from 13 species of fungi in the Botanical Garden

| Fungus species | Cm | Ca | Cd | Pc | Plc | Plo | Tp | Ar | Mh | Lu | Pu | Crm | Ps | Others | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mycodrosophila* spp. | 2 | - | - | - | 2 | 2 | 2 | - | - | 27 | - | - | 6 | 2 | 43 |
| *D. trivittata* | - | - | - | - | 9 | 247 | 12 | 6 | - | - | - | - | 13 | 1 | 288 |
| *D. sexvittata* | 65 | 6 | - | 46 | 33 | 96 | 104 | 68 | 34 | 5 | 99 | 43 | 1127 | 55 | 1781 |
| *D. alboralis* | 4 | 1 | - | 1 | 1 | - | 8 | 1 | - | 19 | 1 | - | 8 | - | 44 |
| *D. confusa* | 112 | 1 | 1 | 1 | - | - | - | - | - | - | 9 | 1 | 244 | - | 369 |
| *D. testacea* | 574 | 150 | 11 | 38 | 2 | 4 | 3 | 5 | - | 113 | 59 | 6 | 12 | 24 | 1001 |
| *D. histrio* | 7 | 2 | - | 1 | - | - | - | - | - | - | - | - | - | - | 10 |
| *D. brachynephros* | 986 | 639 | 43 | 226 | 7 | 46 | 9 | 24 | 18 | 19 | 92 | 26 | 12 | 73 | 2220 |
| *D. unispina* | 200 | 25 | 2 | 30 | 1 | 6 | 5 | 13 | - | 2 | 16 | 2 | 4 | 4 | 310 |
| *D. nigromaculata* | 173 | 105 | 10 | 42 | - | 2 | 1 | 4 | 1 | 1 | - | - | 5 | 3 | 347 |
| *D. immigrans* | 74 | 4 | - | - | - | - | - | - | - | - | - | - | 9 | 3 | 90 |
| Others | 99 | 45 | 2 | 5 | 3 | 1 | 2 | 3 | - | 2 | 1 | 2 | 18 | 3 | 186 |
| Total | 2296 | 978 | 69 | 390 | 58 | 404 | 146 | 124 | 53 | 188 | 277 | 80 | 1458 | 168 | 6689 |

Cm: *Coprinus micaceus*, Ca: *C. atramentarius*, Cd: *C. disseminatus*, Pc: *Psathyrella candolleana*, Plc: *Pleurotus cornucopiae*, Plo: *Pl. ostreatus*, Tp: *Tricholomopsis platyphylla*, Ar: *Armillariella mellea*, Mh: *Mycena haematopus*, Lu: *Lentinellus ursinus*, Pu: *Pluteus cervinus*, Crm: *Crepidotus mollis*, Ps: *Polyporellus squamosus*.

from the fungi of Tricholomataceae, especially from *Pleurotus ostreatus*. *D. alboralis* and three species of *Mycodrosophila*, *M. poecilogastra*, *M. japonica*, and *M. shikokuana*, were collected from *Lentinellus ursinus* frequently.

Table 6 shows the result of collections in the Nopporo Natural Forest. *D. trivittata* was collected mostly from *Pleurotus ostreatus* and *Creolophus spathulatus*, but *D. sexvittata* was collected from a variety of fungi. *D. alboralis* was collected frequently from *C. spathulatus* and *D. brachynephros* and *D. testacea* from *P. ostreatus* or *Colybia* sp..

Table 6. Numbers of individuals of the five leading species collected from the five main fungi in the Nopporo Natural Forest.

| Fungus species | Plo | Co | Lg | Crm | Cs | Others | Total |
|---|---|---|---|---|---|---|---|
| *D. trivittata* | 55 | - | 8 | - | 41 | 5 | 109 |
| *D. sexvittata* | 56 | 81 | 258 | 57 | 171 | 49 | 672 |
| *D. alboralis* | 2 | 4 | - | 3 | 19 | 1 | 29 |
| *D. testacea* | 29 | 5 | - | - | - | 15 | 49 |
| *D. brachynephros* | 8 | 15 | - | 2 | - | 5 | 30 |
| Others | 12 | 3 | 24 | 6 | 8 | 13 | 66 |
| Total | 162 | 108 | 290 | 68 | 239 | 88 | 955 |

Plo, Crm: cf. Table 5, Co: *Colybia* sp., Lg: *Leucopaxillus giganteus*, Cs: *Creolophus spathulatus*.

Table 7. Numbers of individuals of the five leading species collected from the six main fungi in the Moiwa Natural Forest.

| Fungus species | Plc | Plo | Ou | Td | Pp | Cs | Others | Total |
|---|---|---|---|---|---|---|---|---|
| *M. poecilogastra* | 1 | 6 | - | 2 | 57 | 1 | - | 67 |
| *D. trivittata* | 414 | 1246 | 120 | - | - | 3 | 1 | 1784 |
| *D. sexvittata* | 158 | 110 | 147 | 2 | - | 50 | 14 | 481 |
| *D. alboralis* | 2 | 2 | 2 | 29 | 57 | 4 | 6 | 102 |
| *D. testacea* | 1 | 151 | 1 | - | - | - | 2 | 155 |
| Others | - | 20 | 4 | - | 6 | 1 | 17 | 48 |
| Total | 576 | 1535 | 274 | 33 | 120 | 59 | 40 | 2637 |

Plc, Plo, Cs: cf. Tables 5 and 6, Ou: *Oudemansiella mucida*, Td: *Tricholomopsis decola*, Pp: *Polyporellus picipes*.

Table 7 shows the collected number of individuals from the main fungi in the Moiwa Natural Forest. *D. trivittata* also showed a clear preference for the fungi of *Pleurotus*, and it was obtained also from *Oudemansiella mucida* in considerable number. *D. sexvittata* was also collected from the above three species of fungi, but it did not so depend on the fungi of *Pleurotus*. *D. alboralis* was collected mainly from *Tricholomopsis decora* and *Polyporellus picipes*, but *M. poecilogastra* was mainly from *P. picipes*. These two fungi grew 2 m distant to each other in the same period (September 18), then these two species seem to differ in their fungus preference somewhat.

Table 8. Numbers of individuals of the six leading species collected from the eight main fungi in the Nakagawa Experimental Forest of Hokkaido University.

| Fungus species | Rc | Ru | Lp | Al | Ap | Ls | Ty | Plo | Others | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| *D. sexvittata* | 202 | 56 | 5 | 61 | 72 | - | 5 | 15 | 28 | 444 |
| *D. confusa* | 33 | 13 | 24 | - | - | 3 | 157 | - | 15 | 245 |
| *D. testacea* | 58 | 67 | 74 | 40 | 30 | 298 | 1201 | 23 | 51 | 1842 |
| *D. histrio* | 4 | 2 | - | 1 | - | 6 | 37 | - | 2 | 52 |
| *D. brachynephros* | 3 | - | - | 4 | 1 | 1 | 8 | - | 2 | 19 |
| *D. unispina* | 13 | 7 | - | 6 | 17 | 2 | 36 | - | 12 | 93 |
| Others | - | 1 | 5 | 3 | - | 6 | 14 | 10 | 2 | 41 |
| Total | 313 | 146 | 108 | 115 | 120 | 316 | 1458 | 48 | 112 | 2736 |

Rc: *Russula cyanoxantha*, Ru: *R.* sp., Lp: *Lactarius piperatus*, Al: *Amanita longistriata*, Ap: *A. phalloides*, Ls: *Laccinum scabrum*, Ty: *Tylopilus plumbeoviolaceus*, Plo: cf. Table 5.

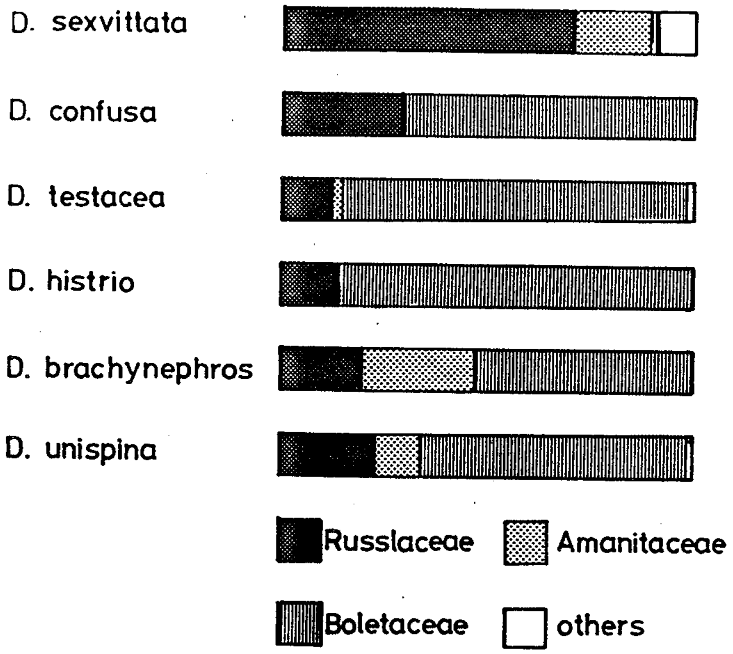

Fig. 3. Proportions of individuals of the leading species attracted to the main families of fungi in August in the Nakagawa Experimental Forest.

Table 8 gives the result of collections in the Nakagawa Experimental Forest, and Fig. 3 shows proportion of individuals of the leading species attracted to the main families of fungi based on the result of collections only in August. D. sexvittata was collected from the fungi of Russulaceae and Amanitaceae in good number, but few from fungi of Boletaceae. The other species, D. confusa, D. testacea, D. histrio, D. brachynephros, and D. unispina, showed strong preference for Boletaceae, and they differed in their fungus preference somewhat. The first three species were seldom collected from the fungi of Amanitaceae, but the last two were collected from them frequently.

In conclusion, *D. trivittata* has a narrow preference for Tricholomataceae, especially for the genus *Pleurotus*. Both of *D. sexvittata* and *D. alboralis* feed and breed on various fungi, but the former rather specializes to Tricholomataceae. Four species of the *immigrans* radiation, *D. testacea*, *D. histrio*, *D. brachynephros*, and *D. unispina*, have very similar fungus preferences to each others, but a little difference was observed between the first two and the last two. *D. confusa* resembles to above four species in the preference for Coprinaceae and Boletaceae, but differs from them in the preference for Aphyllophorales. *M. poecilogastra* prefers the fungi of Aphyllophorales more than the above species.

## Preference for fresh and decayed materials

Tables 9, 10, 11, 12, and 13 give changes of drosophilid fauna from appearance to decay out of three species of fungi, *Pluteus cervinus*, *Polyporellus squamosus*, and *Pleurotus cornucopiae*. *D. sexvittata* was clearly attracted to fresh fungi just after the appearance, and *D. trivittata* also showed the same trend. On the other hand, *D. brachynephros* and *D. testacea* preferred decayed fungi. *D. confusa* was collected simultaneously with *D. sexvittata* from *P. squamosus* in June, 1973, but from rather decayed stage of the same fungus in 1974.

The fungi of *Coprinus* are deliquescent; they begin

Table 9. Numbers of individuals of each species collected on *Pluteus cervinus* on different days following its appearance at May 29, 1974.

| Date | May 29 | 30 | June 1 | 3 | Total |
|---|---|---|---|---|---|
| D. *sexvittata* | 16 | 20 | - | - | 36 |
| D. *testacea* | 1 | - | 3 | 4 | 8 |
| D. *brachynephros* | - | - | 2 | 1 | 3 |
| D. *unispina* | - | 1 | 1 | - | 2 |
| D. *nigromaculata* | - | 1 | 1 | - | 2 |
| Total | 17 | 22 | 7 | 5 | 51 |

Table 10. Numbers of individuals of each species collected on *P. cervinus* on different days following its appearance at July 19, 1974.

| Date | Jul. 19 | 20 | 21 | 22 | 24 | 26 | Total |
|---|---|---|---|---|---|---|---|
| D. *sexvittata* | - | 31 | 6 | 1 | - | - | 38 |
| D. *testacea* | - | - | - | 1 | 3 | - | 4 |
| D. *brachynephros* | - | 2 | 5 | 18 | 8 | - | 33 |
| Total | - | 33 | 11 | 20 | 11 | - | 75 |

Table 11. Numbers of individuals of each species collected on *Polyporellus squamosus* on different days following its appearance at June 1, 1973.

| Date | June 1 | 4 | 5 | 6 | 7 | 11 | 12 | 13 | Total |
|---|---|---|---|---|---|---|---|---|---|
| D. *sexvittata* | 30 | 113 | 161 | 189 | 114 | 42 | 33 | 4 | 686 |
| D. *confusa* | - | 15 | 9 | 18 | 20 | 21 | 7 | 1 | 91 |
| Total | 30 | 128 | 170 | 207 | 134 | 63 | 40 | 5 | 777 |

Table 12. Numbers of individuals of each species collected on P. squamosus on different days following its appearance at June 3, 1974.

| Date | June 3 | 4 | 5 | 7 | 8 | 10 | 14 | 16 | Total |
|---|---|---|---|---|---|---|---|---|---|
| D. sexvittata | 3 | 5 | 13 | 24 | 20 | - | 1 | - | 66 |
| D. alboralis | 1 | - | 1 | - | - | - | 1 | - | 3 |
| D. confusa | - | - | 1 | - | 4 | 19 | 1 | - | 25 |
| D. testacea | - | - | 1 | - | - | 2 | 1 | 2 | 6 |
| D. histrio | - | - | - | - | - | - | - | 2 | 2 |
| Total | 4 | 5 | 16 | 24 | 24 | 21 | 4 | 4 | 102 |

Table 13. Numbers of individuals of each species collected on Pleurotus cornucopiae on different days following its appearance at July 12, 1974.

| Date | July 12 | 13 | 15 | 16 | 17 | 19 | 20 | 21 | Total |
|---|---|---|---|---|---|---|---|---|---|
| D. trivittata | 8 | 1 | 13 | - | 2 | - | - | - | 24 |
| D. sexvittata | 70 | 28 | 7 | 2 | - | - | - | - | 107 |
| D. testacea | - | - | - | - | - | 1 | - | - | 1 |
| D. brachynephros | 2 | 1 | 1 | 1 | - | 1 | 1 | - | 7 |
| D. unispina | - | - | - | 1 | - | - | - | 1 | 2 |
| Total | 80 | 30 | 21 | 4 | 2 | 2 | 1 | 1 | 141 |

to melt and decay one or two days after the appearance. Then, the drosophilid flies which are attracted well to these fungi are assumed to prefer decayed fungi. As shown in Table 5, the member of the immigrans radiation were collected from the fungi of *Coprinus* considerably.

A comparison was made between the collected number of individuals from fleshy fungi and that by traps using fermenting banana as bait (Momma, 1965; Beppu, 1976; Beppu and Toda, 1976). It is clear that species of the *Hirtodrosophila* radiation were not attracted to fermenting banana, but species of the *immigrans* radiation, *D. confusa*, *D. testacea*, *D. histrio*, *D. brachynephros*, and *D. unispina*, were attracted well to that.

## 2. Laboratory experiment

### *Adult mortality and egg productivity on different foods*

Table 14 shows the mean survival periods of each species on different foods for ten days and Table 15 shows number of eggs oviposited. All species survived well on the yeast medium, banana and the fresh *Pleurotus cornucopiae*. But on the agar medium and the fresh *Agaricus bisporus* they can not live longer. On the decayed *P. cornucopiae*, *D. immigrans*, *D. nigromaculata*, *D. sexvittata* and *D. trivittata* died soon after the start of culture, but *D. brachynephros*, *D. testacea*, and *D. confusa* survived rather longer.

Egg productivity of *D. immigrans* was the highest on banana, and nextly on the yeast medium. Egg productivity of *D. nigromaculata* was the highest on the yeast medium and nextly on banana. *D. brachynephros* and *D.*

Table 14. Mean survival periods of seven species on six kinds of foods for ten days.

| Food | agar | yeast | banana | fresh *Pleurotus* | decayed *Pleurotus* | fresh *Agaricus* |
|---|---|---|---|---|---|---|
| *D. immigrans* | 2.9 | 10.0 | 10.0 | 7.5 | 1.0 | 2.9 |
| *D. nigromaculata* | 5.9 | 10.0 | 9.2 | 8.5 | 2.1 | 5.1 |
| *D. brachynephros* | 5.0 | 10.0 | 8.9 | 9.3 | 6.2 | 6.2 |
| *D. testacea* | 4.9 | 10.0 | 9.4 | 10.0 | 7.7 | 7.9 |
| *D. confusa* | 4.9 | 10.0 | 8.7 | 9.5 | 7.9 | 4.5 |
| *D. sexvittata* | 2.1 | 10.0 | 5.6 | 9.1 | 3.0 | 6.0 |
| *D. trivittata* | 2.6 | 10.0 | 8.2 | 9.3 | 1.5 | 2.1 |

Table 15. Numbers of eggs oviposited by each species on six kinds of foods for ten days.

| Food | agar | yeast | banana | fresh *Pleurotus* | decayed *Pleurotus* | fresh *Agaricus* |
|---|---|---|---|---|---|---|
| *D. immigrans* | 14 | 817 | 1687 | 324 | 83 | 1 |
| *D. nigromaculata* | 168 | 1171 | 723 | 439 | 161 | 171 |
| *D. brachynephros* | 51 | 367 | 143 | 184 | 526 | 8 |
| *D. testacea* | 109 | 726 | 288 | 326 | 1390 | 120 |
| *D. confusa* | 189 | 522 | 525 | 375 | 483 | 147 |
| *D. sexvittata* | 150 | 243 | 68 | 490 | 57 | 76 |
| *D. trivittata* | 35 | 26 | 2 | 363 | - | - |

*testacea* could produce eggs very well on the decayed *P. cornucopiae*, and nextly on the yeast medium, the fresh *P. cornucopiae*, and banana. The yeast medium, banana, and the decayed *P. cornucopiae* worked well for *D. confusa*. *D. sexvittata* and *D. trivittata* produced eggs most on the fresh *P. cornucopiae*, and the former also well on the yeast medium. The agar medium and the fresh *A. bisporus* seemed to be innutritive for drosophilid flies.

## Preferences of adult flies for decayed and fresh mushrooms

Table 16 gives the result of experiment. *D. trivittata* and *D. sexvittata* were attracted more to the fresh mushroom. *D. sexvittata* oviposited on the decayed mushroom somewhat in addition to the fresh mushroom, but *D. trivittata* avoided the decayed mushroom for oviposition. *D. alboralis* was attracted and oviposited on every conditions of mushroom rather equally. *D. immigrans*, *D. nigromaculata*, *D. brachynephros*, *D. testacea*, and *D. confusa* preferred the decayed mushroom for feeding and ovipositing.

## Oviposition sites

Table 17 shows the proportion of eggs oviposited on the stipe, upper surface of pileus, and lamella, for each species. Species which preferred the decayed mushroom, *D. immigrans*, *D. nigromaculata*, *D. brachynephros*,

Table 16. Proportions of adult flies attracted to (A) and eggs oviposited on (O) the fresh, intermediate, and decayed Pleurotus cornucopiae.

| | | Fresh | Intermediate | Decayed | Number of eggs oviposited |
|---|---|---|---|---|---|
| D. immigrans | (A) | 14.3 | 41.5 | 44.1 | |
| | (O) | 15.0 | 29.0 | 56.0 | 2046 |
| D. nigromaculata | (A) | 26.4 | 27.9 | 45.7 | |
| | (O) | 23.7 | 27.0 | 49.3 | 367 |
| D. brachynephros | (A) | 25.4 | 31.3 | 43.3 | |
| | (O) | 17.6 | 25.0 | 57.4 | 296 |
| D. testacea | (A) | 25.3 | 29.1 | 45.6 | |
| | (O) | 9.6 | 22.7 | 67.7 | 238 |
| D. confusa | (A) | 37.4 | 27.6 | 35.0 | |
| | (O) | 13.7 | 29.1 | 57.2 | 955 |
| D. alboralis | (A) | 35.3 | 32.9 | 31.8 | |
| | (O) | 38.9 | 27.3 | 33.8 | 139 |
| D. sexvittata | (A) | 69.5 | 13.9 | 16.6 | |
| | (O) | 43.1 | 37.4 | 19.5 | 447 |
| D. trivittata | (A) | 66.1 | 28.3 | 5.6 | |
| | (O) | 61.3 | 38.7 | - | 253 |

D. testacea, and D. confusa, oviposited on the stipe and upper surface of pileus. D. alboralis also showed the same ovipositing habit. But D. sexvittata oviposited into the lamella in addition to the surface of pileus, and D. trivittata almost into the lamella. No significant difference of oviposition sites was observed whether P. cornucopiae was fresh or decayed. On the other hand,

Table 17. Proportions of eggs oviposited on the stipe, upper surface of pileus, and lamella of Pleurotus cornucopiae.

| | Stipe | Pileus | Lamella |
|---|---|---|---|
| D. immigrans | 42.6 | 54.2 | 3.2 |
| D. nigromaculata | 23.2 | 69.7 | 7.1 |
| D. brachynephros | 22.0 | 77.4 | 0.6 |
| D. testacea | 29.9 | 68.8 | 1.3 |
| D. confusa | 53.9 | 40.7 | 5.4 |
| D. alboralis | 22.3 | 77.0 | 0.7 |
| D. sexvittata | 1.1 | 37.1 | 61.8 |
| D. trivittata | - | 2.4 | 97.6 |

on the fresh Agaricus bisporus, all species except for D. trivittata which did not oviposit on this fungus, oviposited almost into the stipe as observed by Shorrocks and Wood (1972).

Preferences of larvae for fresh and decayed mushroom

Table 18 gives the result. All species were attracted to the decayed P. cornucopiae, though less intense in D. sexvittata and D. trivittata.

Larval viability on the yeast-agar-sugar medium

In D. immigrans, D. nigromaculata, and D. brachynephros, about 50% of eggs grew to the adults, but in D. testacea only 8.7% and in D. confusa 0.8%. No adult of *D. sexvittata* and *D. trivittata* came off from this medium.

Table 18. Proportions of larvae attracted to the fresh, intermediate and decayed *Pleurotus cornucopiae*.

| | Fresh | Intermediate | Decayed | No. of larvae |
|---|---|---|---|---|
| *D. immigrans* | 14.6 | 34.1 | 51.2 | 41 |
| *D. nigromaculata* | 4.2 | 21.1 | 74.7 | 71 |
| *D. brachynephros* | 4.4 | 15.6 | 80.0 | 45 |
| *D. testacea* | 8.3 | 26.3 | 65.4 | 133 |
| *D. confusa* | 11.4 | 30.0 | 58.6 | 70 |
| *D. alboralis* | 5.6 | 11.1 | 83.3 | 17 |
| *D. sexvittata* | 4.4 | 50.0 | 45.7 | 46 |
| *D. trivittata* | 11.1 | 40.7 | 48.2 | 81 |

## Discussion

The original feeding habit of Drosophilidae was considered to be saprophagous, since members of various groups fed and bred on decayed or fermenting materials as shown in Part I. But they do not feed and breed on every part~~s~~ under decay or fermentation, but they prefer one substrate over the others. In this study, adults of *D. immigrans* and *D. nigromaculata*, which are a fruit feeder and a herbage feeder respectively, can not survive on the decayed mushroom, though they prefer the decayed mushroom to the fresh mushroom for feeding and ovipositing. These species also feed and breed on the limited species of fungi in the field. They would not adapt to the mushroom for feeding and breeding. *D. testacea* and *D. brachynephros* also prefer the decayed mushroom, but they can survive and produce eggs on it very well. These species and their relatives, *D. histrio* and *D. unispina* feed and breed on various fungi of Agaricales, but seldom on those of Aphyllophorales. *D. confusa* also prefers the decayed *P. cornucopiae* to the fresh one as well as the above species, and it was collected well from fungi of Coprinaceae and Boletaceae for which above species showed a strong preference, but it differs from these species in the preference for the fresh *Polyporellus squamosus* and in the frequent use of fungi of Aphyllophorales for breeding. *D. alboralis* uses various fungi for breeding as well as members of the *immigrans* radiation, but it is attracted to fresh mushrooms in addition to decayed mushrooms. This species is unique in the use of the stipe for breeding.

Among the fungus feeders, *D. sexvittata* and *D. trivittata* are very unique in their preferences for the fresh fungi. *D. sexvittata* has a wide preference for fungi, though it feeds and breeds rather frequently on Tricholomataceae and avoids Coprinaceae, Agaricaceae, or Boletaceae. On the other hand, *D. trivittata* breeds exclusively on Tricholomataceae, especially on the genus *Pleurotus*. Species of *Mycodrosophila* and *D. quadrivittata* seem to have a strong preference for Aphyllophorales, and this preference was also observed by Nishiharu (1978) in Honshû.

The change of feeding habits observed in fungus feeders of the *immigrans*-*Hirtodrosophila* radiation were summarized as follows:

1. Development of preference for fresh fungi in *D. confusa*, *D. alboralis*, *D. sexvittata* and especially in *D. trivittata*.
2. Specialization of fungus preference for Tricholomataceae in *D. sexvittata*, and particuraly in *D. trivittata*.
3. Specialization to Aphyllophorales in *D. quadrivittata* and the members of *Mycodrosophila*.

4. Use of the stipe of fungi for breeding in *D. alboralis*.
5. Use of the lamellae for the oviposition site in *D. sexvittata* and *D. trivittata*.

The development of preference for fresh materials was also observed in herbage feeders, flower feeders, and fruit feeders. Leaf miners of *Scaptomyza* would be evolved from *Scaptomyza* species which had bred on the decayed leaves, as *S. pallida* or *S. consimilis*. Species which use living flowers as its breeding site (Pipkin *et al.*, 1966; Brncic, 1966) would also evolved from species feeding and breeding on fallen flowers. In fungus feeders, gradation of preference was observed from *D. confusa* which showed a slight preference for the fresh fungi to *D. trivittata* which showed a strong preference. In contrast to the preference of adult, the preferences of larvae did not show clear difference among species studied here. Carson and Kaneshiro (1976) considered that nutritive requirement provided by specific host plant or microorganisms may not necessarily be the most essential factor for host selectivity for larval breeding, but ovipositional behavior of the females is the primary mechanism for it.

As a factor which brings development of preference for fresh materials, competitive interactions are considered here. Gilpin (1974) studied intraspecific competition of *D. melanogaster* in the laboratory condition, and observed that the individuals introduced earlier had competitive advantage to those introduced later. Among fungus feeders individuals oviposited earlier may also have advantage, and this may lead species to be attracted to fresh materials.

The specialization of fungus preference in D. sexvittata and D. trivittata was partly due to that some fresh mushrooms are innutritive for adult drosophilid flies as Agaricus bisporus. Fungi of Coprinaceae or Boletaceae also may be innutritive when fresh, as flies were seldom attracted to fresh fungi of these families. The specialization of D. trivittata to the fungi of Pleurotus will be discussed in Part III in relation to ecology of the fly and fungi. Specialization of D. quadrivittata and the members of Mycodrosophila to Aphyllophorales could not be explained in this study. The members of Mycodrosophila are more abundant in southern Japan or tropic regions, and then their preference must be studied there with ecology of the fly and fungi.

The food specialization according to the development of preference for fresh materials was also observed in flower feeders in the neotropical region (Pipkin et al., 1966). Some of them breed on only one plant species (monophagous), and some do on few species (oligophagous).

The ovipositing habit also seems to change in relation to the development of preference for fresh fungi. D. trivittata and D. sexvittata oviposited into lamellae of *P. cornucopiae*, while other species usually oviposited into the caps or stipes. On *Agaricus bisporus*, however, *D. sexvittata* oviposited mainly into the stipes as well as others. Then the use of lamellae for the oviposition site may be developed in relation to the specialization to Tricholomataceae.

*D. sexvittata* and *D. trivittata* are also unique in their egg morphology; their eggs do not have filament (Okada, 1956). It was known that flies which oviposite on fresh or living materials often have eggs with no or modified filaments in Drosophilidae, e.g., *Scaptomyza* graminum, a leaf-miner (Okada, 1968), some of the flower feeding species of *Drosophila* (Patterson and Stone, 1952; Pipkin *et al.*, 1966), or some of *Lissocephala*, specialists to fresh fruits (Lachaise, 1977). The anchor function of the filaments is at least useless for eggs oviposited on fresh and firm substrates.

# PART III

## Abundance, Microdistribution, Seasonal Life Cycle of Fungus Feeding *Drosophila* in and near Sapporo

## Introduction

As described in the former Parts, some drosophilid flies changed their food preference in the course of evolution or speciation. Competitive interaction within and between species and nutritive condition of foods were discussed as factors which bring changes of the food preference. In addition to these factors, ecological factors of both flies and food plants, distribution, abundance, or seasonality, would take an important role in a long history of evolution of food preference. Conversely, food preferences of flies would have deep influences on their distribution, abundance, or seasonality of flies at present. Microdistibution of drosophilid flies were studied by several workers as referred in introduction, but analytical studies on abundance were few. In recent years, seasonality of temperate drosophilid flies was investigated in relation to the seasonal change of their reproductive conditions (Lakovaara *et al.*, 1972; Lumme *et al.*, 1974; Begon, 1976; Lumme, 1978). These studies clarified the seasonal adaptation of drosophilid flies in relation to dormancy. Here, the author clarifies microdistribution, abundance, and seasonal life cycle of fungus feeding drosophilid species and abundance and seasonality of host fungi in and near Sappro, and discusses on their abundance in relation to their food preferences and ecology of the fungi. Further, the author discusses on evolution of their food preferences based on ecology of the flies and host fungi.

## Areas Studied and Methods

The collections of drosophilid flies from fleshy fungi were carried out at seven localities near Sapporo (Fig. 4), the Nopporo Natural Forest (NF), the Moiwa Natural Forest (MF), the Botanical Garden of Hokkaido University (BG), the grove of the campus of Hokkaido University (UC), the windbreak at Shin-Kotoni (SK), the windbreak at Shin-Sapporo (SS), and the larch grove at Shin-Sapporo (SL). The collecting methods for the first three localities were described in Part II. For BG only the data of 1974 are incorporated in this study. UC is the reserved grove occupying about 4,500 m. SK is composed of _Abies sachalinensis_ and _Populus monilifera_, and has 60 m in width. SS is composed of the native

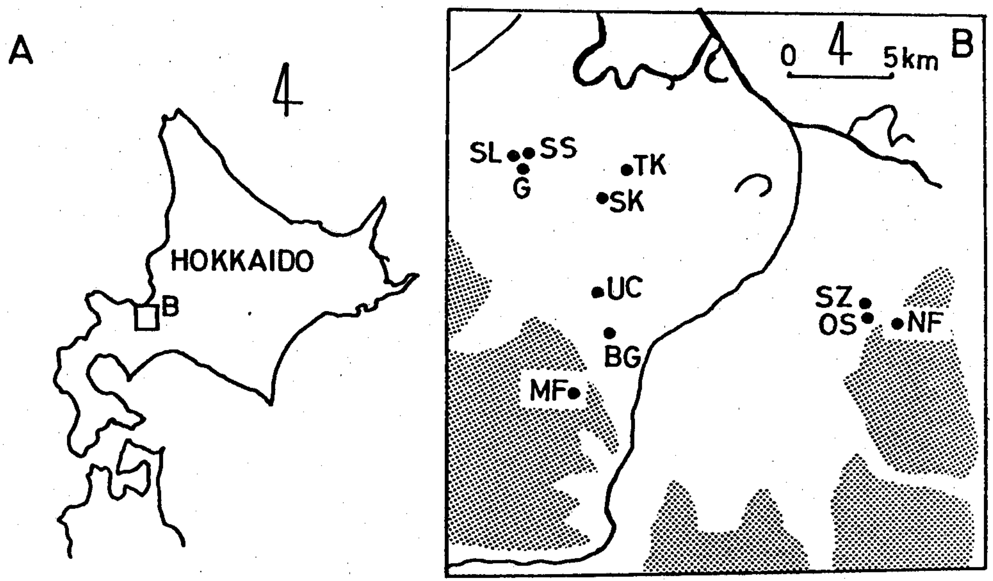

Fig. 4. Collecting localities. Shaded parts suggest the forest regions.

trees and has 80 m in width. Both windbreaks extends several kilometers. LS covers about 2,500 $m^2$. The collecting methods for UC, SK, SS, and SL were the same with those for NF and MF. The collections were made along paths in groves or windbreaks, 225 m in UC, 300 m in SK, 600 m in SS, and 150 m in LS, and were made twice in each month from June to October in 1977.

In order to study the distribution and abundance of fungus feeders which are attracted to fermenting fruits, trap collections using the "retainer trap" baited with fermenting banana were made once for a week in each month from May to October at NF, SK, two residental areas (TK, SZ in Fig. 4), and a bushed area (OS) in 1977, and at UC, SK, SL, and three open areas (two sites at G, $G_1$ and $G_2$, and UCC, neibouring field of UC) in 1978.

To investigate the voltinism, all females collected were dissected under a binocular microscope and examined their reproductive conditions. The criteria of classification of ovarian conditions was given by Watabe and Beppu (1977); Stage I: undeveloped, Stage II: developing, Stage III: mature, and Stage IV: postmature ovaries.

## Results

### Fleshy fungi in the collecting areas

Table 19 shows numbers of the main fleshy fungi which attracted the drosophilid flies frequently in each collecting area. Number of species and amount of fleshy fungi were abundant in the forest areas, NF and MF. BG which consists of an isolated grove also had rich fungus flora, but in other isolated groves or windbreaks, fungus species and their amount were poor, especially no important fungus was found in SL. This would be due to the dry condition of these areas. In fungus species, *Pleurotus ostreatus* was abundant in NF, MF, and BG, and was also found frequently in small groves or windbreaks. *P. cornucopiae* was frequent in NF, MF, and BG. Other fungi of Tricholomataceae seem to be less abundant than the above two species, and seem to show unequal distribution. *Crepidotus mollis* occurs widely, but amount of this fungus is not so large in spite of large individual number, because this fungus is very small. The fungi of *Coprinus* and *Psathyrella* were abundant in BG, but seldom in the other localities. In Aphyllophorales, *Polyporellus squamosus*, *P. picipes*, and *Creolophus spathulatus* were observed frequently in NF, MF, or BG. Fig. 12 presents the seasonal occurrence of the main fungi based on this survey and the survey of the breeding sites in Part I.

Table 19. Number of each fungus species which attracted drosophilid flies well for each collecting area. The abbreviations for localities were shown in text.

| Locality | NF | MF | BG | UC | SK | SS | SL |
|---|---|---|---|---|---|---|---|
| Pleurotus ostreatus | 377 | 1515 | 359 | - | 16 | 60 | - |
| P. cornucopiae | 5 | 520 | 185 | - | - | - | - |
| Armillariella mellea | - | 2 | 15 | 50 | - | 1 | - |
| Oudemansiella mucida | 1 | 162 | - | - | - | - | - |
| Tricholomopsis platyphylla | - | 3 | 76 | - | - | - | - |
| Crepidotus mollis | 80 | 40 | 823 | 60 | - | - | - |
| Pluteus cervinus | 13 | - | 5 | - | - | - | - |
| Coprinus micaceus | - | 360 | 1990 | - | 250 | - | - |
| C. atramentarius | - | - | 135 | - | - | - | - |
| Psathyrella candolleana | 8 | 50 | 553 | 30 | - | 5 | - |
| Polyporellus squamosus | - | 3 | 29 | - | - | - | - |
| P. picipes | - | 34 | 4 | - | - | - | - |
| Creolophus spathulatus | 260 | 20 | - | - | - | - | - |

*Pleurotus ostreatus*, *P. cornucopiae*, *Pluteus cervinus*, *Coprinus micaceus*, and *Polyporellus squamosus* were found through seasons, but other fungi were found only in particular seasons.

### Abundance and microdistribution of drosophilid flies

Table 20 shows number of individuals of the main drosophilid species collected from fleshy fungi at the seven collecting localities. At NF, MF, and BG, a considerable number of flies was collected, but at the small groves or windbreaks only a small number was obtained. The drosophilid fauna were rather similar among the localities compared with the great difference in fungus flora. In general, the members of the *immigrans-Hirtodrosophila* radiation were dominant. In addition, members of *Leucophenga*, *Sophophora*, and *Scaptodrosophila* were sometimes collected.

Among the fungus feeders of *Hirtodrosophila* radiation *D. sexvittata* and *D. trivittata* were very abundant in forest areas and BG. *D. alboralis* and *M. poecilogastra* were collected frequently, but *D. quadrivittata*, *D. makinoi*, *M. japonica*, *M. shikokuana*, and *M. takachihonis* were very rare in and near Sapporo. In addition to them, *D. macromaculata*, *D. nokogiri*, *D. pseudonokogiri*, *D. kangi*, *M. bifibulata*, and *M. gratiosa* were known in Hokkaido (Beppu *et al.*, 1977), but they were not collected in this survey. *D. busckii*,

Table 20. Numbers of individuals of the main drosophilid flies collected from fleshy fungi at each localities. Abbreviations for localities were shown in text.

| | NF | MF | BG | UC | SK | SS | SL |
|---|---|---|---|---|---|---|---|
| *Hirtodrosophila* radiation | | | | | | | |
| *M. takachihonis* | - | 6 | - | - | - | - | - |
| *M. shikokuana* | 4 | - | 2 | 1 | - | - | - |
| *M. japonica* | 4 | - | 8 | - | - | 2 | - |
| *M. poecilogastra* | 2 | 67 | 13 | - | - | - | - |
| *D. trivittata* | 109 | 1784 | 232 | - | - | 2 | - |
| *D. sexvittata* | 672 | 481 | 627 | 16 | 8 | 13 | - |
| *D. alboralis* | 29 | 102 | 24 | 1 | - | - | - |
| *D. quadrivittata* | 5 | 2 | 2 | - | - | - | - |
| *D. makinoi* | - | - | 4 | - | - | - | - |
| *immigrans* radiation | | | | | | | |
| *D. confusa* | 20 | 11 | 216 | 2 | 4 | - | - |
| *D. testacea* | 49 | 155 | 734 | 6 | 11 | 12 | 5 |
| *D. histrio* | 1 | 6 | 9 | - | - | - | - |
| *D. brachynephros* | 30 | 4 | 1516 | 25 | 15 | 12 | 16 |
| *D. unispina* | 14 | 6 | 231 | - | - | 1 | - |
| *D. nigromaculata* | 2 | 5 | 235 | 1 | 1 | - | - |
| *D. immigrans* | - | 2 | 52 | - | - | - | - |
| Others | 14 | 6 | 114 | - | 4 | - | - |
| Total | 955 | 2637 | 4019 | 52 | 43 | 42 | 21 |

a domestic species, was not collected from fleshy fungi, but it was obtained by trap collections.

Four species of the *immigrans* radiation, *D. confusa*, *D. testacea*, *D. brachynephros*, and *D. unispina*, were collected abundantly from fleshy fungi, but *D. histrio* was rare. Besides them, *D. kunzei*, *D. limbata*, and *D. bizonata* were recorded from northern or southern Hokkaido, but they were not collected in Sapporo.

The abundance of drosophilid flies in a collecting area corresponded to that of fungi; both of flies and fungi were abundant in NF, MF, and BG, but scarce in UC, SK, SS, and SL. In NF and MF, the individuals of species belonging to the *Hirtodrosophila* radiation, which were composed mostly by *D. sexvittata* and *D. trivittata*, were collected more frequently than those of the *immigrans* radiation. Their dominance would be due to the abundance of fungi belonging to Tricholomataceae for which *D. sexvittata* and *D. trivittata* showed a strong preference. The abundance of individuals belonging to the *immigrans* radiation in BG also would be due to the abundance of deliquescent fungi of *Coprinus* and *Psathyrella* for which they have a strong preference (cf. Table 5).

Fig. 5 shows the relationship of the number of species of flies of each radiation collected in each station (three in NF, two in MF, five in BG, and one in each of UC, SK, SS, and SL) and species number of fleshy fungi which attracted the flies in that station. By the results of NF, MF, and BG, the number of species of *Hirtodrosophila* radiation correlated positively with the number of fungus species, but the results of SK and SL slipped off from the line. On the other hand, the

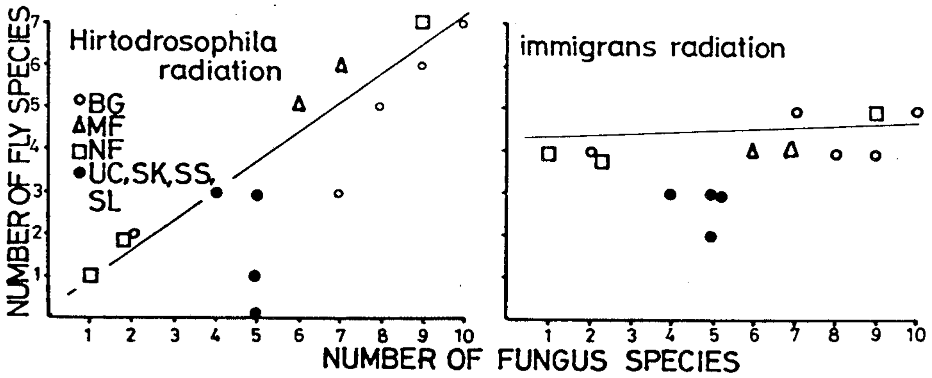

Fig. 5. Relationship of number of fly species collected and number of fungus species which attracted the flies in collecting stations.

species number of the _immigrans_ radiation was stable irrespective of the number of fungus species in NF, MF, and BG, but number of fly species in isolated groves or windbreaks was small.

Fig. 6 gives the relationship of the number of fly species and the number of individuals for each radiation. The individual number collected in a station would correlate with the productivity of that station, i.e., the amount of fungi. In the _Hirtodrosophila_ radiation the species number correlated positively with the individual number, but in the _immigrans_ radiation the species number was stable in NF, MF, and BG.

In the _Hirtodrosophila_ radiation, _D. sexvittata_ distributed rather widely, though collected number was few in UC, SK, and SS. In the _immigrans_ radiation, _D. testacea_ and _D. brachynephros_ occurred widely, and these

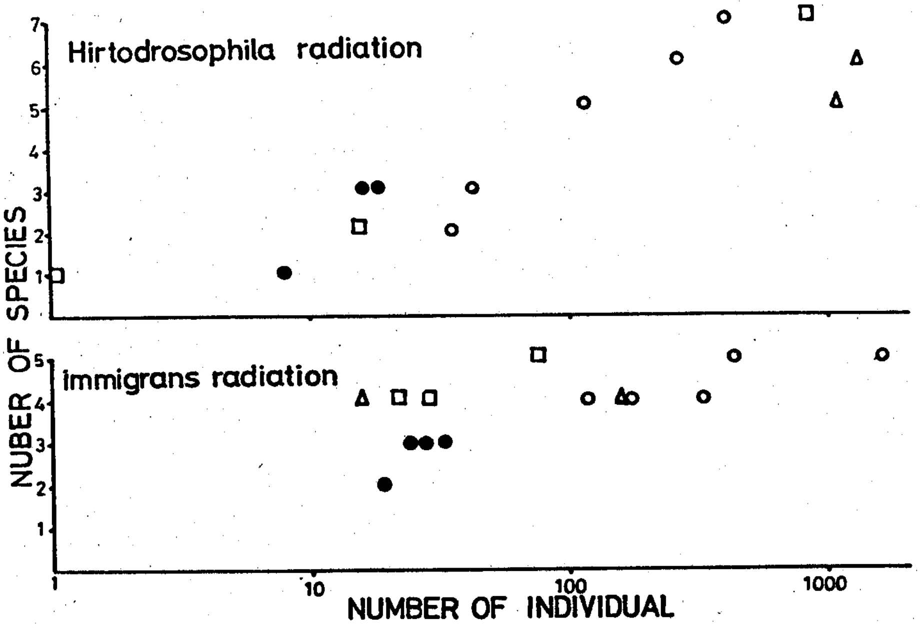

Fig. 6. Relationship between number of fly species and number of individuals for each of the Hirtodrosophila and immigrans radiations in collecting stations.

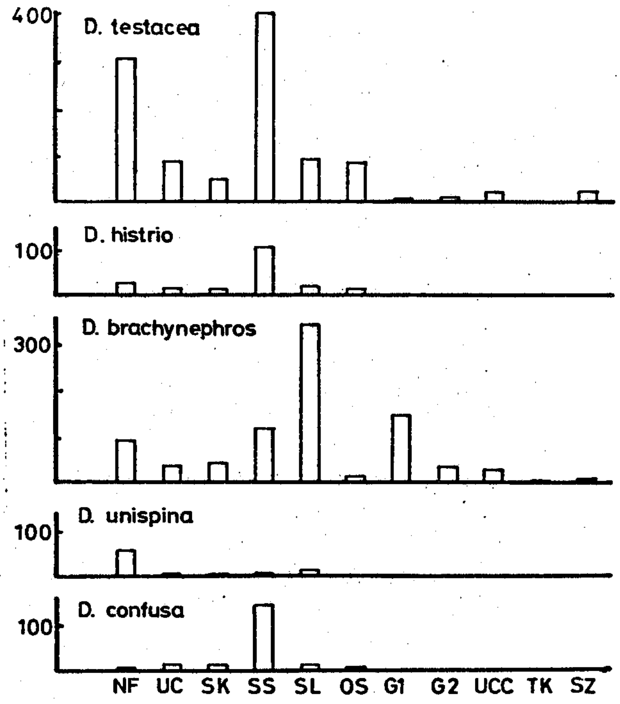

Fig. 7. Numbers of individuals of fungus feeders collected by traps in each collecting station.

two species were also collected abundantly by traps in forests, isolated groves, and windbreaks (Fig. 7). But *D. histrio*, *D. unispina*, and *D. confusa* which were seldom collected from fungi in isolated groves and windbreaks were collected rather frequently by traps in those areas. In open areas, $G_1$, $G_2$, and UCC, *D. testacea* and *D. brachynephros* were found sometimes, but the other three species were not collected.

### *Seasonal life cycles*

Fig. 8 shows the seasonal change of female reproductive conditions of *D. sexvittata* with absolute individual numbers counted for each ovarian stage for BG, MF, and NF. The fluctuation of male number which is represented only for BG strictly corresponded to that of females. This species had three distinct peaks in population size, in early June, late July, and early September, though the June peak is small in MF and NF. The individuals of hibernate generation ($G_h$) become to be attracted to fungi at the late May or early June, and soon develop their ovaries. They decrease in number during June and mostly disappear by early July. Their offspring, the first generation ($G_1$), appear with undeveloped ovaries in early July in BG, but somewhat later in NF and MF. The population of $G_1$ reaches maximum in late July. These individuals soon develop their ovaries and breed in late July and early August. The drop of

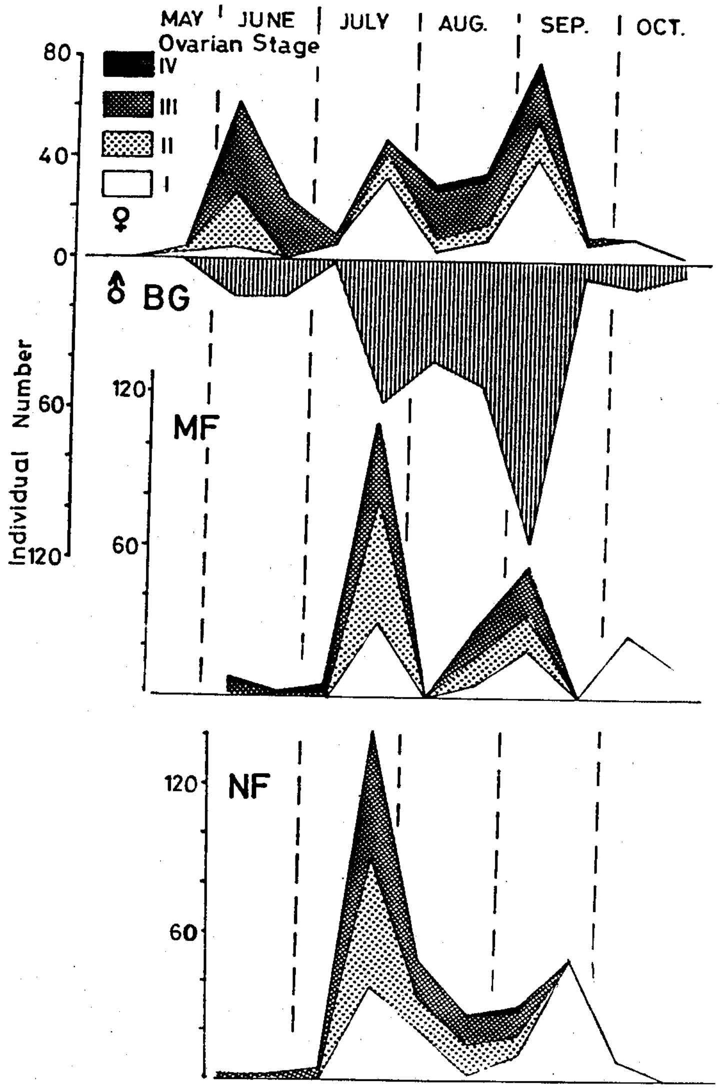

Fig. 8. Seasonal changes of female reproductive conditions and male number of D. sexvittata in BG, MF, and NF.

collected number in August is conspicuous in NF and MF, but not in BG. The flies of the next generation, $G_2$, would appear from mid August. Some parts of them which emerged by early September seem to develop their ovaries and reproduce, but the remaining parts emerged after early September seem to enter the reproductive diapause without ovarian development. All individuals of the third generation would enter the reproductive diapause. Therefore, this species seems to pass through two or three generations per year.

Fig. 9 shows the results on D. trivittata for BG, NF, and MF. The collected number of this species fluctuated seasonaly very much. In BG only few individuals were collected by July, and in NF only a few was collected. Only the result of MF allows to follow the seasonal life cycle of this species. This species shows very similar seasonal life cycle with D. sexvittata, though mature females of $G_2$ or $G_3$ of this species were observed till late September, somewhat later than D. sexvittata. This may suggest greater longevity of $G_2$, or later start of the diapause. This species also passes through two or three generations per year.

Fig. 10 shows the seasonal changes of female reproductive conditions of D. testacea, D. brachynephros, and D. unispina based on the collections in BG. The $G_h$ individuals of these species were collected only in small number. The $G_1$ young adults appear in early July,

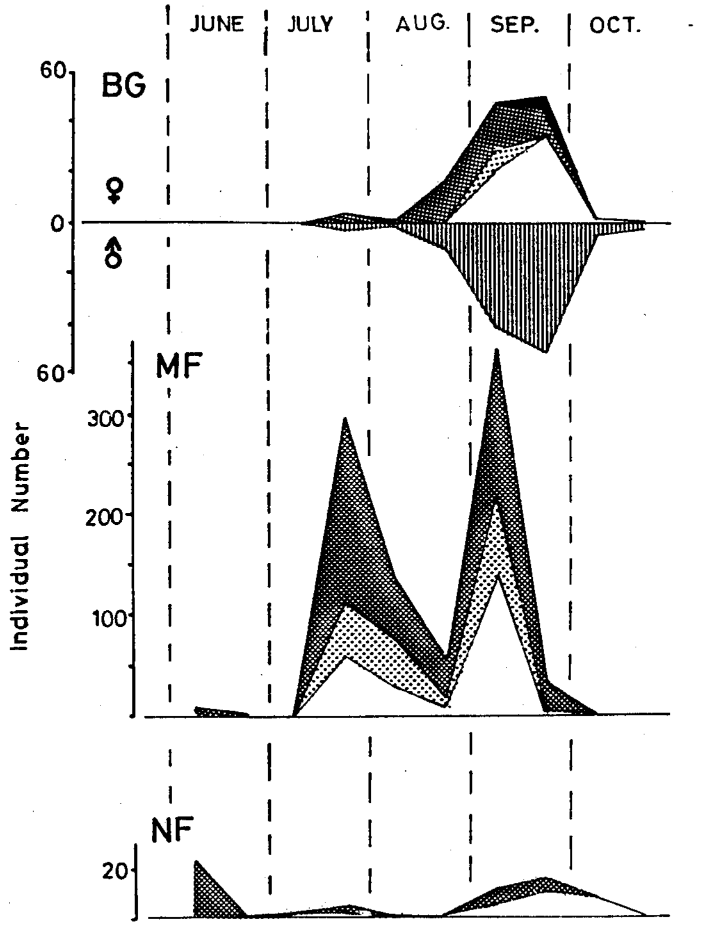

Fig. 9. Seasonal changes of female reproductive conditions and male number of D. trivittata in BG, MF, and NF. Legends cf. Fig. 8.

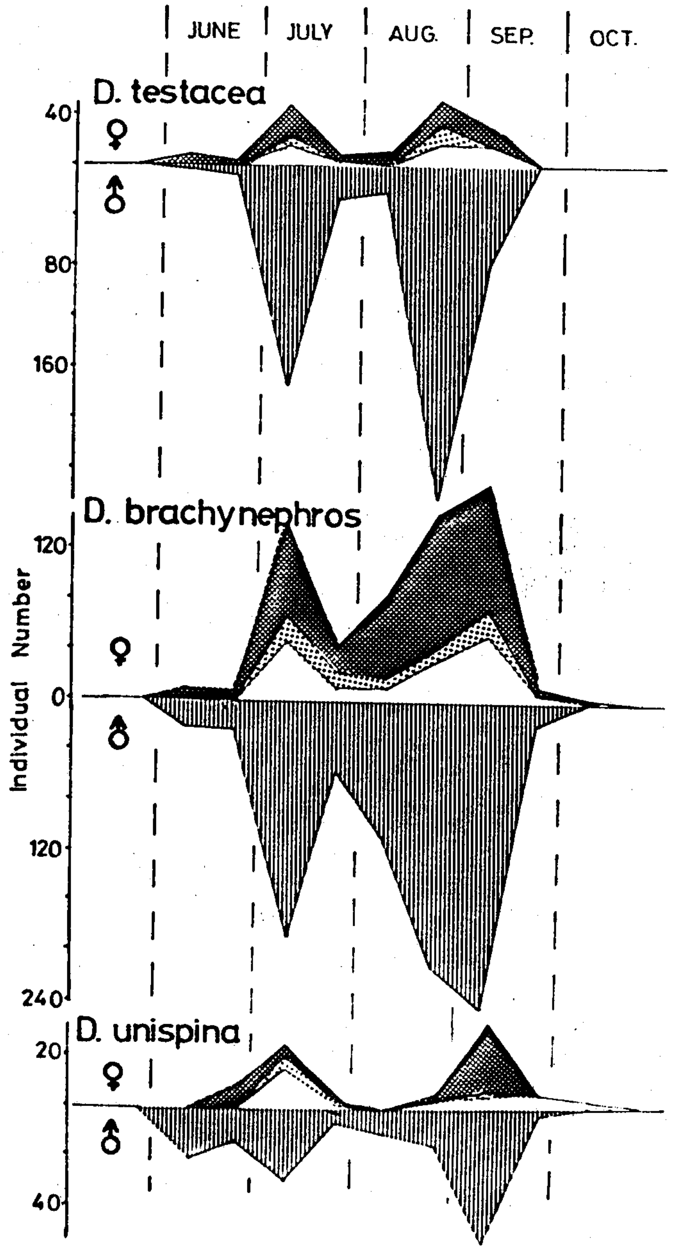

Fig. 10. Seasonal changes of female reproductive conditions and male numbers of D. testacea, D. brachynephros, and D. unispina in BG. Legends cf. Fig. 8.

somewhat earlier than those of *D. sexvittata* and *D. trivittata*. After $G_1$, the alternation of generations was difficult to follow because of the overlap of generations. According to results of weekly collections using traps (Watabe and Beppu, 1977; Watabe, 1977; Kimura *et al.*, 1978; Watabe *et al.*, unpubl.), these species pass mainly three, but partially two, generations per year in and near Sapporo. The individuals of these species emerged after early September seem to enter the reproductive diapause. The diapausing individuals of these species seldom collected from fleshy fungi in autumn, though fleshy fungi were rather abundant in that season. However, by trap collections, the diapausing flies of *D. confusa*, *D. testacea*, *D. histrio*, *D. brachynephros* and *D. unispina* were collected abundantly in September or October. This may suggest the change of food preference when they eneter the diapause.

Figs. 11, 12, 13, 14, 15, and 16 present the seasonal host changes in *D. trivittata*, *D. sexvittata*, *D. alboralis*, *D. confusa*, *D. testacea*, and *D. brachynephros*. *D. trivittata* which has a strong preference for *Pleurotus* used *P. ostreatus* through the whole breeding seasons, and also used some fungi of Tricholomataceae when they existed. On the other hand, *D. sexvittata* scarcely used the fungi of *Pleurotus*, but it used widely the other fungi of Tricholomataceae and some

| | MAY | | JUNE | | JULY | | AUG. | | SPT. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ● | ● | ● | ● | ● | ● | ● | ● | ○ |
| Pl. cornucopiae | | ○ | ○ | | ● | ● | ○ | ● | | ○ |
| Armillariella mellea | | ● | ● | ● | ○ | | | ● | ● | ○ |
| Oudemansiella mucida | | | ● | ○ | | ● | | ● | ● | |
| Ou. radicata | | | | | ○ | ○ | | | ○ | ○ |
| Tricolomopsis platyphylla | | ○ | ● | | | | | | | ● |
| Colybia erythropus | | | ● | ● | | | | | | |

Fig. 11. Seasonal change of host fungi for breeding in D. trivittata. White circle: fungus existed but not used for breeding, black circle: used for breeding.

| | MAY | | JUNE | | JULY | | AUG. | | SPT. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ○ | ○ | ○ | ○ | ○ | ● | ● | ○ | ○ |
| Pl. cornucopiae | | ○ | ○ | | ○ | ● | ○ | ○ | | ○ |
| Armillariella mellea | | ○ | ● | ● | ● | | | ● | ● | ○ |
| Oudemansiella mucida | | | ● | ● | | ○ | | ● | ● | |
| Ou. radicata | | | | | ● | ● | | | ○ | ○ |
| Tricolomopsis platyphylla | | ○ | ● | | | | | | | ● |
| Colybia erythropus | | | ● | ● | | | | | | |
| Mycena haematopus | | | ● | ○ | | | ○ | ○ | | |
| Pholiota squarrosa | | | | ● | ● | | ○ | | | |
| Crepidotus mollis | | | ○ | ○ | | ● | ● | | | |
| Pluteus cervinus | | ○ | ○ | ● | ○ | ● | ● | ● | ○ | |
| Coprinus micaceus | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Co. atramentarius | | | ○ | ○ | ○ | ○ | | | ○ | ○ |
| Psathyrella candolleana | | | ● | ○ | ● | ○ | ○ | | ○ | |
| Polyporellus squamosus | ○ | ○ | ● | ● | ● | ● | ○ | ○ | ○ | ○ |
| Po. picipes | | | | ○ | ○ | | ○ | | | ○ |

Fig. 12. Seasonal change of host fungi for breeding in D. sexvittata. Legends cf. Fig. 11.

|  | MAY |  | JUNE |  | JULY |  | AUG. |  | SPT. |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ |
| Pl. cornucopiae |  | ○ | ○ |  | ○ | ○ | ○ | ○ |  | ○ |
| Armillariella mellea |  | ● | ● | ● | ○ |  |  | ○ | ○ | ○ |
| Oudemansiella mucida |  |  | ● | ● |  | ○ |  | ○ | ○ |  |
| Ou. radicata |  |  |  |  | ○ | ○ |  |  | ○ | ○ |
| Tricolomopsis platyphylla |  | ○ | ● |  |  |  |  |  |  | ○ |
| Colybia erythropus |  |  | ○ | ● |  |  |  |  |  |  |
| Mycena haematopus |  |  | ○ | ○ |  |  | ○ | ○ |  |  |
| Pholiota squarrosa |  |  |  | ● | ● |  | ○ |  |  |  |
| Crepidotus mollis |  |  | ○ | ○ |  | ○ | ● |  |  |  |
| Pluteus cervinus |  | ○ | ○ | ● | ● | ○ | ● | ○ | ○ |  |
| Coprinus micaceus | ○ | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ |
| Co. atramentarius |  |  | ○ | ○ | ○ | ○ |  |  | ○ | ○ |
| Psathyrella candolleana |  |  | ● | ○ | ● | ○ | ○ |  | ○ |  |
| Polyporellus squamosus | ○ | ○ | ○ | ● | ● | ○ | ○ | ○ | ○ | ○ |
| Po. picipes |  |  |  | ● | ○ |  | ○ |  |  | ○ |

Fig. 13. Seasonal change of host fungi for breeding in D. alboralis. Legends cf. Fig. 11.

other families when they existed. D. alboralis showed a similar tendency with D. sexvittata, but its breeding was observed less frequently in late summer and autumn (the breeding season correspinding to $G_1$ and $G_2$). Three species of the immigrans radiation, which preferred decayed fungi, were observed breeding from June to September on various fungi, and they did not avoid the fungi of Pleurotus.

The hibernating flies of several species were found in various hibernacles in winter. In cliff shelters along streams M. poecilogastra, D. alboralis

| | MAY | | JUNE | | JULY | | AUG. | | SPT. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ● | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ |
| Pl. cornucopiae | | ○ | ● | | ○ | ○ | ○ | ○ | | ○ |
| Armillariella mellea | | ● | ● | ● | ● | | | ○ | ○ | ○ |
| Oudemansiella mucida | | | ○ | ○ | | ○ | | ○ | ○ | |
| Ou. radicata | | | | | ○ | ○ | | | ○ | ○ |
| Tricolomopsis platyphylla | | ○ | ○ | | | | | | | ○ |
| Colybia erythropus | | | ○ | ○ | | | | | | |
| Mycena haematopus | | | ○ | ○ | | | ○ | ○ | | |
| Pholiota squarrosa | | | | ○ | ○ | | ○ | | | |
| Crepidotus mollis | | | ○ | ○ | | ○ | ○ | | | |
| Pluteus cervinus | | ○ | ○ | ○ | ● | ○ | ○ | ○ | ○ | |
| Coprinus micaceus | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Co. atramentarius | | | ○ | ● | ○ | ○ | | | ○ | ○ |
| Psathyrella candolleana | | | ○ | ○ | ○ | ○ | ○ | | ○ | |
| Polyporellus squamosus | ○ | ○ | ● | ● | ● | ● | ● | ○ | ○ | ○ |
| Po. picipes | | | | ○ | ○ | | ○ | | | ○ |

Fig. 14. Seasonal change of host fungi for breeding in D. confusa. Legends cf. Fig. 11.

D. quadrivittata, D. brachynephros, and D. unispina were found, and among the lichens on barks of trees D. sexvittata and D. trivittata were collected. Only one male of D. testacea was collected in a crevice of bark. Most females collected in winter had undeveloped overies and were not inseminated, but females of D. alboralis passed winter in the inseminated state. A very small fraction of hibernating females was occupied by females with post-mature ovaries.

|  | MAY |  | JUNE |  | JULY |  | AUG. |  | SPT. |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ○ | ● | ● | ● | ○ | ● | ○ | ● | ○ |
| Pl. cornucopiae |  | ○ | ● |  | ○ | ● | ● | ● |  | ○ |
| Armillariella mellea |  | ○ | ● | ○ | ○ |  |  | ○ | ○ | ○ |
| Oudemansiella mucida |  |  | ○ | ○ |  | ○ |  | ○ | ○ |  |
| Ou. radicata |  |  |  |  | ○ | ○ |  |  | ○ | ○ |
| Tricolomopsis platyphylla |  | ○ | ○ |  |  |  |  |  |  | ○ |
| Colybia erythropus |  |  | ○ | ○ |  |  |  |  |  |  |
| Mycena haematopus |  |  | ○ | ○ |  |  | ○ | ○ |  |  |
| Pholiota squarrosa |  |  |  | ○ | ○ |  | ○ |  |  |  |
| Crepidotus mollis |  |  | ○ | ○ |  | ○ | ● |  |  |  |
| Pluteus cervinus |  | ○ | ● | ○ | ● | ● | ● | ● | ○ |  |
| Coprinus micaceus | ○ | ○ | ● | ○ | ○ | ○ | ○ | ● | ○ | ○ |
| Co. atramentarius |  |  | ○ | ○ | ○ | ● |  |  | ○ | ○ |
| Psathyrella candolleana |  |  | ○ | ○ | ○ | ○ | ● |  | ○ |  |
| Polyporellus squamosus | ○ | ○ | ● | ● | ● | ● | ○ | ○ | ○ | ○ |
| Po. picipes |  |  |  | ○ | ○ |  | ○ |  |  | ○ |

Fig. 15. Seasonal change of host fungi for breeding in *D. testacea*. Legends cf. Fig. 11.

| | MAY | | JUNE | | JULY | | AUG. | | SPT. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| Pleurotus ostreatus | ○ | ○ | ● | ○ | ● | ● | ● | ○ | ● | ○ |
| Pl. cornucopiae | | ○ | ○ | | ○ | ○ | ○ | ○ | | ○ |
| Armillariella mellea | | ○ | ○ | ○ | ○ | | | ○ | ● | ○ |
| Oudemansiella mucida | | | ○ | ○ | | ○ | | ○ | ○ | |
| Ou. radicata | | | | | ○ | ○ | | | ○ | ○ |
| Tricolomopsis platyphylla | | ○ | ○ | | | | | | | ○ |
| Colybia erythropus | | | ○ | ○ | | | | | | |
| Mycena haematopus | | | ○ | ○ | | | ○ | ○ | | |
| Pholiota squarrosa | | | | ○ | ○ | | ○ | | | |
| Crepidotus mollis | | | ○ | ○ | | ● | ● | | | |
| Pluteus cervinus | | ○ | ○ | ○ | ● | ● | ○ | ○ | ○ | |
| Coprinus micaceus | ○ | ○ | ● | ● | ● | ○ | ● | ● | ● | ● |
| Co. atramentarius | | | ● | ● | ● | ○ | | | ● | ○ |
| Psathyrella candolleana | | | ● | ● | ● | ○ | ○ | | ○ | |
| Polyporellus squamosus | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Po. picipes | | | | ○ | ○ | | ○ | | | ○ |

Fig. 16. Seasonal change of host fungi for breeding in D. brachynephros. Legends cf. Fig. 11.

# Discussion

The roles of inter- and intraspecific competitions and nutritive conditions of foods in the evolution of food preference were discussed in the preceding part. Here the role of ecology of food plants is discussed. Emlen (1973) considered the food specialization and generalization from the viewpoints of evolutionary ecology, and noted the food specialization is due to the overall food abundance and some other factors. The fungus feeding drosophilids are multivoltine and their breeding takes place continuously from June to September in Hokkaido. Then, their food specialization is possible only when one kind of food (fungus) is abundant temporally as well as spatially. Five species of fungi were observed continuously from spring to autumn in and near Sapporo, but only *Pleurotus ostreatus* and *P. cornucopiae* were observed rather widely and abundantly. The specialization of *D. trivittata* to this genus is enforced by the ubiquity of this genus. It is very interesting that *D. sexvittata* and *D. alboralis* which have a very wide preference for fungi seem to avoid this genus for breeding. This may be a result of interspecific competition with *D. trivittata*. For *D. sexvittata* and *D. alboralis* there is no available fungus in and near Sapporo to which these species specialize, as far as these species remain multivoltine and breed continuously through seasons.

According to the competitive exclusion principle, two species having the same niche can not live together. In drosophilid assemblage, ecological niches of sibling or closely related species usually resemble each other, and they frequently occur sympatrically. Dobzhansky and Pavan (1950) considered each form of life exploits some ecological niches, in one of which it has a net superiority over all competitors. Similarly, Reynoldson and his collaborators (Reynoldson, 1966; Reynoldson and Davies, 1970; etc.) studied triclad populations in England, and reached the same conclusion. He called the food on which a species takes a superiority over all competitors the "food refuge". The fungus feeders of the *Hirtodrosophila* radiation have different preferences for fungi, though overlapped, and they seem to have the "food refuge"; *D. trivittata* for the fungi of *Pleurotus*, *D. sexvittata* for the other fungi of Tricholomataceae, *D. alboralis* for stipe of fungi for larval breeding, and *D. quadrivittata* for fungi of Aphyllophorales, though members of *Mycodrosophila* seem to have similar preferences with *D. quadrivittata*. It is conceibable that the number of these species in a area correlates with the food diversity and food quantity in that area.

The members of the *immigrans* radiation which have very similar fungus preferences to each other coexist in a area with limited fungus species and amount of fungi. It was not known how they coexist. They may have different preferences for yeasts or bacteria. *D. brachynephros* can grow to adult on the yeast medium, but *D. testacea* and *D. confusa* have only a slight viability on this medium. Kaneko (1960) studied yeast preferences of these flies in BG, and observed that *D. testacea* and *D. brachynephros* have different preferences for yeasts, though *D. brachynephros* and *D. unispina* show similar preferences. Toda (1973a) observed that *D. brachynephros* and *D. unispina* have different habitat preferences; the former was abundant in open areas as well as forests, but the latter was collected mostly in forests.

Ayalá (1969, 1970, 1971) investigated interspecific competition of several *Drosophila* species in the laboratory condition, and observed that some pairs of species coexisted during long periods. He studied the survivorship and productivity in competitive coexistence of *D. willistoni* and *D. pseudoobscura*, and concluded that the coexistence was allowed by the frequency dependent fitness. The relative fitness of two species under competition are inversely related to the relative frequency of these species. Gilpin and Justice (1972) reinterpreted these data, and showed the data fit a non-linear competition model. Under natural conditions such competitive coexistence may or may not occur.

Food preference of a species evolved through interactions with its environments has much influence on ecology of that species. The abundance of a fungus feeding drosophilid in a area was affected by the abundance of favorite fungi of the species in question. For example, *D. trivittata* and *D. sexvittata* were abundant at where the fungi of Tricholomataceae were abundant. Especially *D. trivittata* seems to be affected by the presence of the fungi of *Pleurotus*. *D. trivittata* can not maintain its population in the isolated groves or windbreaks where fungi of *Pleurotus* were scarce. In contrast, *D. sexvittata* which have a wider preference seems to be able to maintain its population in those areas, though small in number. The abundance of *D. brachynephros* and *D. testacea* in isolated groves and windbreaks needs another explanation. These species may have a physiological advantage in such small groves characterized by higher temperature and desiccation than the forest. Moreover, as *D. brachynephros* has a preference for open areas (Toda, 1973a), and as *D. testacea* seems to have great migratory ability (Kimura *et al.*, 1978), the open areas do not barrier the migration of these species, and new individuals may be supplied from surrounding forests frequently.

The voltinism of drosophilid flies was generally determined by the length of period free from diapause, the total cummulative temperature of this period, and the developmental speed of flies. In temperate areas they pass through several generations (four to six in *D. obscura* and *D. subobscura* in England; Begon, 1976), but in north areas they pass only one or two generations (Finish drosophilids; Lakovaara *et al.*, 1972; Lumme *et al.*, 1974, Lumme, 1978).

*D. trivittata* and *D. sexvittata* pass two or three generations per year in Sapporo, but *D. testacea*, *D. brachynephros*, and *D. unispina* do mainly three, but partially two, gnerations. The appearance of $G_1$ of *D. trivittata* and *D. sexvittata* is later somewhat than that of *D. testacea* or *D. brachynephros*, and this results in fewer generations per year. These fungus feeding species enter the reproductive diapause in early September. The diapause of drosophilid flies is usually controlled by photoperiods and temperature (Lumme *et al.*, 1974; Lumme, 1978; Minami *et al.*, in press).

# PART IV

# Abundance, Microdistribution, and Seasonal Life Cycle of Herbage Feeding Drosophila in and near Sapporo

## Introduction

The herbage feeding drosophilid species occupy an important part in drosophilid fauna in Hokkaido. This assemblage consisted of species of the *Scaptomyza*, some of *Sophophora*, *Lordiphosa*, and *Drosophila*. All species except for *D. nigromaculata* are seldom collected by traps using fermenting banana, but they were collected abundantly by net sweeping on herbage layer (Suzuki, 1955; Okada, 1956). These species have very similar food preferences for each other as reported in Part I. In this part the author reports their abundance, microdistribution, and seasonal life cycle based on the sweeping collections in and near Sapporo, further he wishes to discuss on their coexistence and food generalization.

## Areas Studied and methods

To investigate the abundance and microdistribution, the collection were carried out at eight localities in and near Sapporo, the Nopporo Natural Forest (NF), the Botanical Gardens (BG), the campus of Hokkido University (UC), the windbreak at Shin-Kotoni (SK), the windbreak at Shin-Sapporo (SS), the larch grove at Shin-Sapporo (LS), and the grass land at Shin-Sapporo, (G), The vegetation and geography of those areas were described in Part III. In NF two collecting stations (NFA, NFB), in BG four stations (BGA, BGD, BGE, in groves, BGF in lawn), in UC three stations UCA, UCB in groves, UCC in a field ), and in G two stations ($G_1$, $G_2$) were set. In other localities only one collecting station was set. Each collecting station occupied about 100 $m^2$, and the collections were made monthly from May to October. Each collection was composed of 400 times of net sweeping on the herbage layer. The net used was 36 cm in diameter, and the shaft was 1 m in length. The collections were carried out at UCA and UCB for three years from 1972 to 1974, in BG in 1973, in NF in 1973 and 1974. At UCC, SK, SS, SL, and G, the collections were made in 1978.

In order to analyse seasonal life cycles of these herbage feeders, collections were made weekly at BG in 1974 and at NF in 1977. The collections were made at eight stations (five in groves, BGA: collecting periods, Apr. 22 - Oct. 28, BGB: Apr. 30 - Oct. 28, BGC: Apr. 30 - Aug. 27, BGD: Apr 30 - Aug. 19, BGE: Apr. 30 - Sep. 3, and three in lawn, BGF: Apr. 22 - Oct. 28, BGG and BGH: Sep. 3 - Oct. 28) in BG and at ten stations in NF from May 9 to Sep. 26. Net sweeping was made 100 times for each collection at each station. The collected females were dissected for the study of the seasonal change of the reproductive conditions. The criteria for the ovarian stages were referred in Part III.

## Abundance and Phenology of Herbage Plants

The relative abundance and phenology of the main undergrowth plants at each station were shown in Table 21. Species of *Anemone* and *Adonis amurensis* are spring ephemeral; they fall down in May and June, and go to decay. *Osmorhiza aristata*, *Heracleum dulce*, *Anthriscus sylvestris* and *Trillium* spp. fall little later, and decayed laeves of accidentary fallen specimens of these plants are observed frequently in June. *Smilacina japonica*, *Maianthemum delatatum*, and *Lilium cordatum* var. *glehni* are observed from spring to autumn, and the decay of these plants are also extensive in June. *Trifolium repens* and its decay were observed rather through seasons. *Cryptotaenia japonica* falls in autumn and goes to decay. Table 22 gives records of the main herbage plants utilized as the breeding sites by herbage feeding *Drosophila*. In conclusion, the decayed plants are abundant in May or June, and in other months the fallen plants sometimes dry up.

Table 21. Main undergrowth plants at collecting stations and their phenology.

+++: dominant, ++: abundant, +: common

| Station | NFA<br>NFB | BGA<br>BGB<br>BGC | BGD | BGE | BGF<br>BGG<br>BGH<br>UCC | UCA<br>UCB | SK | SS | SL | $G_1$ | $G_2$ | Phenology |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Anemone raddeana* | | | | | | +++ | | | | | | IV-VI |
| *A. flaccida* | + | +++ | | + | | | | | | | | IV-VI |
| *Osmorhiza aristata* | + | ++ | | + | | | | | | | | IV-VIII |
| *Anthriscus sylvestris* | | + | +++ | + | | | | | | | | IV-VIII,X |
| *Heracleum dulce* | | + | + | +++ | | + | + | | | | | V-VIII |
| *Smilacina japonica* | ++ | + | | | | | | + | | | | V-X |
| *Lilium cordatum* var. *glehni* | + | + | ++ | ++ | | + | | | | | | V-IX |
| *Trillium kamtschaticum* | | + | + | + | | + | | + | | | | IV-VII |
| *T. smallii* | ++ | | | | | | | | | | | V-X |
| *Petasites japonicus* var. *giganteus* | + | | | | | | | | | | | V-X |
| *Trifolium repens* | | | | | +++ | | + | | | + | + | IV-XI |
| *Poa pratensis* | | | | | +++ | | | | +++ | | | IV-XII |
| *Cryptotaenia japonica* | +++ | ++ | ++ | | | | | | | | | VI-X |
| *Rudbeckia laciniata* | | | | | | | +++ | | | | | VI-X |
| *Solidago altissima* | | | | | | | | | | +++ | | VI-X |
| *Antemisia montana* | | | | | | | | | | | +++ | V-X |

Table 22. Records of the main plants utilized as breeding sites by drosophilid species

| | May | | June | | July | | Aug. | | Sept. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| *Anemone flaccida* | | + | + | | | | | | | |
| *Osmorhiza aristata* | | | + | | | | | | | |
| *Anthriscus sylvestris* | | + | + | + | | | | | | |
| *Heracleum dulce* | | + | + | + | | | | | | |
| *Smilacina japonica* | | | + | + | | | | | | |
| *Lilium cordatum* var. *glehni* | | | + | + | | | | | | |
| *Trillium smallii* | | | + | + | | | | | | |
| *Maianthemum delatatum* | | | + | | | | | + | | |
| *Petasites japonicus giganteus* | | | + | | | + | | | | |
| *Cryptotaenia japonica* | | | | | | | | | + | |
| *Trifolium repens* | | | | | + | + | | + | + | |

## Results

A total of 4,771 individuals representing 29 species were collected by the monthly collections. Table 23 shows the number of the 13 higher ranked species for each station in each year. Most of them were herbage feeders, and some of fungus feeders or fruit feeders such as *D. brachynephros*, *D. testacea* or *D. auraria* were collected. In the genus *Scaptomyza*, *S. pallida* was dominant in isolated groves or windbreaks, and also in open areas. *S. consimilis*, *S. polygonia*, and *S. okadai* were sometimes collected in isolated groves, and rather rare in forests of NF. *D. collinella*, *D. tenuicauda*, and *D. mommai* were abundant in NF, In isolated groves *D. collinella* was frequently, and *D. tenuicauda* was sometimes found, but no specimen of *D. mommai* was collected. *D. nipponica*, *D. magnipectinata*, and *D. nigromaculata* were collected equally in both of forest and grove.

### Seasonal life cycle

#### *Scaptomyza pallida*

The seasonal change of female reproductive age structure is demonstrated (Fig. 17) with absolute individual numbers counted for each ovarian stage based upon the results of weekly collections in BG. Fluctuation

Table 23. Numbers of individuals of the main species obtained by monthly collections

|  | NFA |  | NFB |  | BGA | BGD | BGE | BGF | UCA |  |  | UCB |  |  | UCC | SK | SS | SL | $G_1$ | $G_2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 73 | 74 | 73 | 74 | 73 | 73 | 73 | 73 | 72 | 73 | 74 | 72 | 73 | 74 | 77 | 77 | 77 | 77 | 77 | 77 |
| S. pallida | 14 | 35 | 4 | 17 | 257 | 74 | 14 | 461 | 126 | 63 | 1012 | 52 | 63 | 150 | 435 | 43 | 2 | - | 29 | 8 |
| S. consimilis | 1 | 2 | 4 | 1 | 1 | 6 | 6 | - | 27 | 8 | 95 | 23 | 15 | 14 | - | - | - | - | - | - |
| S. polygonia | 1 | 1 | - | - | 3 | - | - | 3 | 8 | 10 | 2 | 30 | 11 | 1 | - | - | - | - | - | - |
| S. okadai | - | - | - | - | - | 6 | 1 | - | 1 | 1 | - | 1 | - | 1 | - | - | - | - | - | - |
| D. collinella | 41 | 68 | 54 | 78 | 14 | 2 | 1 | - | 2 | 3 | 30 | 3 | 1 | 5 | - | 21 | 36 | - | - | - |
| D. mommai | 24 | 18 | 1 | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| D. nipponica | 27 | 97 | 4 | 6 | 22 | 87 | 6 | - | 14 | 6 | 26 | 11 | 1 | 9 | 2 | 92 | 4 | - | 6 | - |
| D. magnipectinata | 7 | 2 | 24 | 3 | 23 | 35 | 2 | - | 10 | 8 | 10 | 5 | 1 | 4 | - | 15 | 2 | - | - | - |
| D. nigromaculata | 9 | 17 | 4 | 18 | 24 | 66 | 17 | - | 26 | 15 | 130 | 11 | 3 | 22 | 1 | 28 | 6 | - | 3 | - |
| D. tenuicauda | 5 | 29 | 19 | 14 | 1 | 3 | 4 | - | - | - | - | 1 | - | - | - | - | - | - | - | - |
| others | 1 | 9 | 6 | 9 | 10 | 9 | 2 | - | 9 | 11 | 12 | 19 | 5 | 17 | 12 | 12 | 13 | 8 | 3 | - |
| Total | 130 | 278 | 120 | 148 | 355 | 288 | 53 | 464 | 223 | 125 | 1317 | 156 | 100 | 223 | 450 | 211 | 63 | 8 | 41 | 8 |

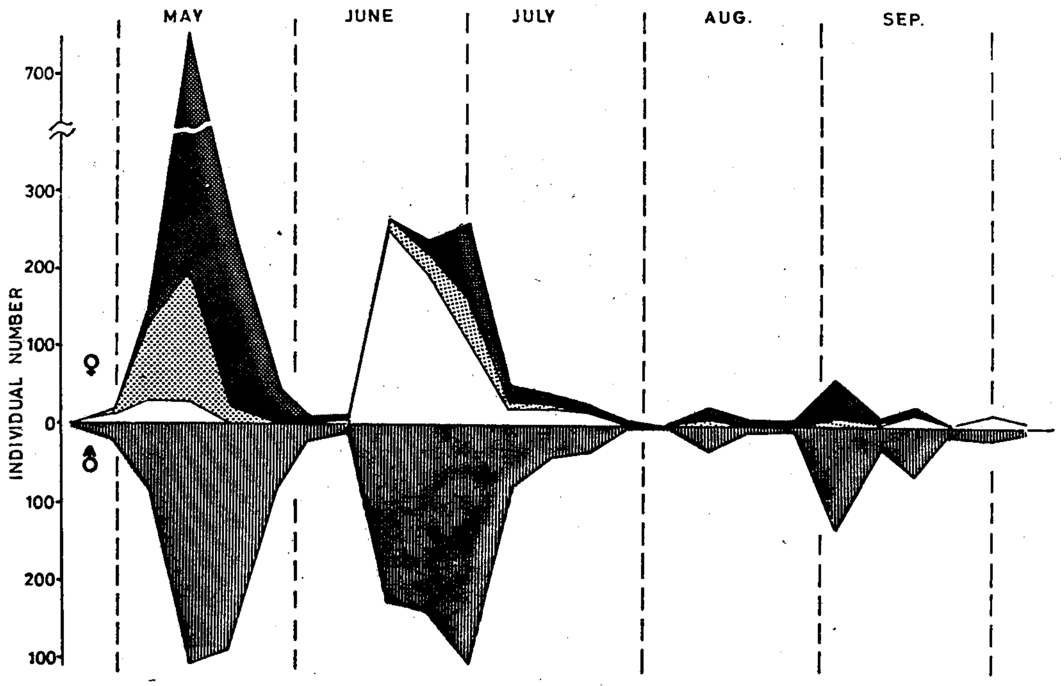

Fig. 17. Seasonal change of female reproductive conditions and male number of S. pallida in the weekly collections in BG. Legends cf. Table 8.

of accompanied male numbers strictly corresponds to that of females, exhibiting two conspicuous peaks in May and in mid to late June. Post-hibernation adults appear from late April, two or three weeks later after snow thawing, to mid May. Their ovaries are first rudimentary, but soon develop. In mid May the population reaches the first peak composed mostly of reproductively mature females. Thereafter, the individual number decreases rapidly and drops to a very low level in early June just before the emergence of $G_1$. Although $G_1$

adults continue to emerge from mid June to late July, they are the most abundant in mid to late June. The newly emerged $G_1$ females also develop rapidly their ovaries and perform second breeding. At this phase the figure shows an abrupt drop of individual number. However, the drop does not necessarily indicate the actual decrease of population size, but rather a dilution of population density by dispersal from patchy herbage stands to uniform white clover stands extending over lawns. Due to the reduced sample sizes and further to the partial overlap of generations caused by the prolongation of each generation, it becomes somewhat difficult to distinguish the later generations for each other. $G_1$ females are supposed to live in mature condition at least till mid August. $G_2$ begins to emerge from early or mid August, and $G_2$ females emerged before mid September develop their ovaries. $G_3$ begins to emerge from mid September, probably together with the last part of $G_2$. These females emerged after mid September seem to enter the reproductive diapause. Then this species passes through mainly three, but partially two, generations per year.

Fig. 18 illustrated the seasonal change of female age structure separately for each collecting station, except the white clover stands for which the data of two or three stations are combined. It is first noticed that the first peak of $G_h$ appears syn-

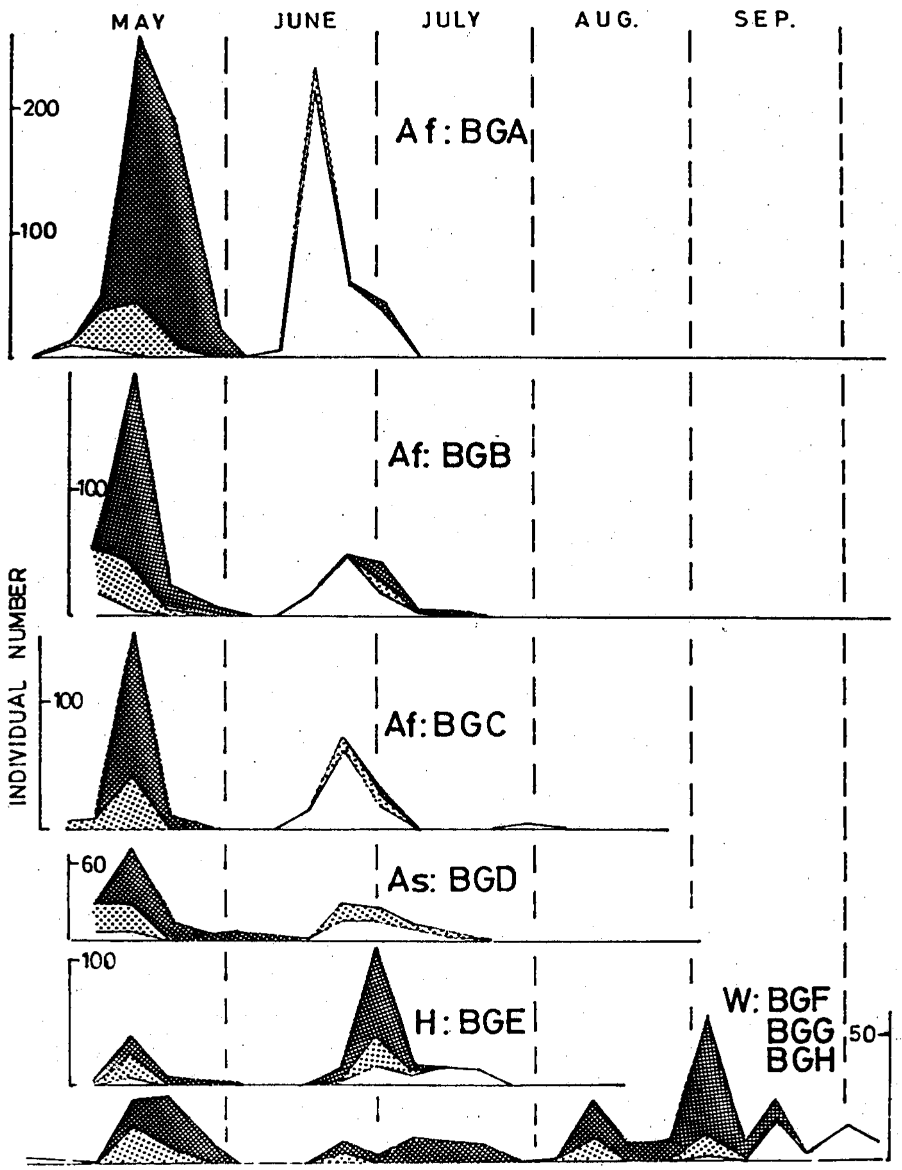

Fig. 18. Seasonal changes of female reproductive conditions of S. pallida at four different host plant stands; Af: A. flaccida stand, As: A. sylvestris stand, H: H. dulce stand, W: white clover stand.

chronously in mid May at every vegetations. The patterns of emergence of $G_1$ females are identical for three stations of *A. flaccida* stands (BGA, BGB, BGC). At the *Anthriscus* stand (BGD), the age structure of $G_1$ is slightly different from that at *A. flaccida* stands, including not only the females with undeveloped ovaries but also those with developing ones. Here $G_1$ starts from late June, one or two weeks later than at *A. flaccida* stands, but is compensated by a prolongation till mid July. The emergence does not show such a burst as at *A. flaccida* stands. The pattern at *Heracleum dulce* stand (BGE) is characterized by the temporal accumulation of mature females in early July, though the appearance of reproductively undeveloped females is nearly the same as at the *A. sylvestris* stand. It is supposed that the variation detected among the three herbage stands reflects different life cycles of the respective host plants, which are referred previously. *A. flaccida* begins to decay nearly synchronously since mid May and is withered up already in early June. On the other hand, *A. sylvestris* and *H. dulce* usually begin to decay in late May and their decay was not so abrupt as *A. flaccida*. The earlier emergence with a conspicuous peak of $G_1$ at *A. flaccida* stands reflects the earlier and rapid decay of the host plant. A remarkable scarcity of $G_1$ females with developing or mature ovaries is to be interpreted by the complete disappearance of the host plant at the stands by the time of emergence, which must have driven the flies to emigrate soon after the emergence. Conversely, the decaying of A. sylvestris and H. dulce, starting later and proceeding slowly, causes the delayed emergence without a detectable peak of $G_1$ at both stands. The presence of the host plants at that time permits the newly emerged flies to stay there for a while. However, these flies also emigrate elsewhere, especially to white clover stands, as the host plants are withering up. Consequently, virtually no flies are collected from these three herbage stands after July.

On the other hand, at white clover stands of lawns (BGF, BGG, BGH), the flies are continuously, though in moderate individual numbers, collected throughout the whole season, reflecting the annual availability of the host plant, white clover, there. The appearance of newly emerged $G_1$ females corresponds to those observed at the A. sylvestris and H, dulce stands, from late June to mid July. In contrast to the scarcity of these immature females, a considerable number of mature females appears from mid July to early August. This accumulation of mature females, which is regarded as a characteristic feature of $G_1$ at white clover stands, must be caused by the immigration from other host plant stands as mentioned above. The alternation of generation after $G_1$ was taken mostly at white clover stands at lawn.

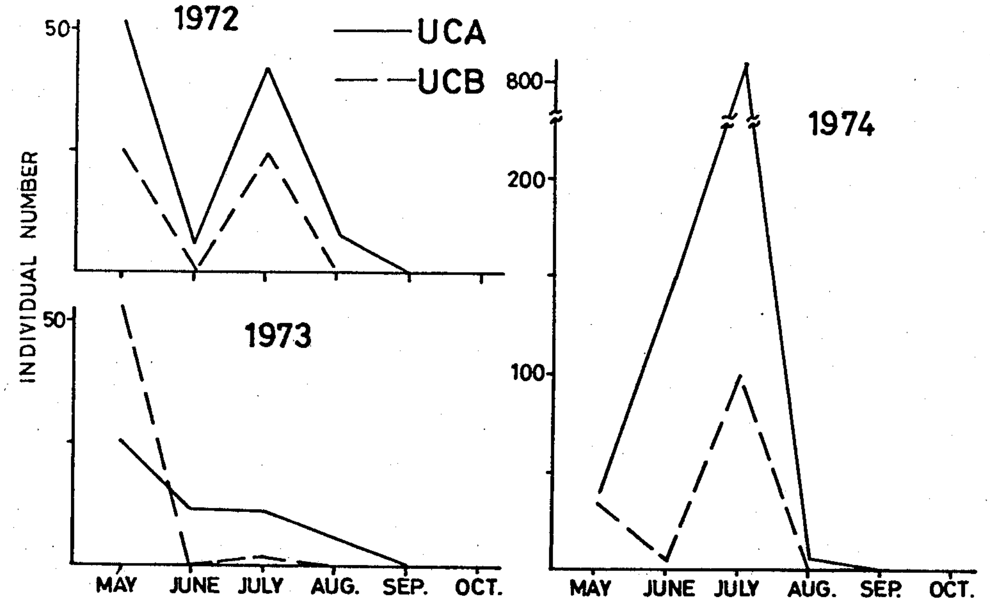

Fig. 19. Seasonal fluctuations of S. pallida at UCA and UCB for three years.

Fig. 19 shows the monthly change of collected number at UCA and UCB for three years. As reported above, the peak of May corresponded to $G_h$, and that of July to the $G_1$. In 1972 both peaks were conspicuous, and in 1974 the July peak was very large. But in 1973 the July peak was negligible compared with the May peak. This would be due to the scarcity of rainfall. As shown in Fig. 20, the rainfall in June, when larvae of this species grew, was very small in 1973, and the breeding materials (decayed leaves) dried up. Similarly, small peak was also observed for populations of this species in BG in 1973. In 1974, the population of this species was very large at UCA. This tendency was observed

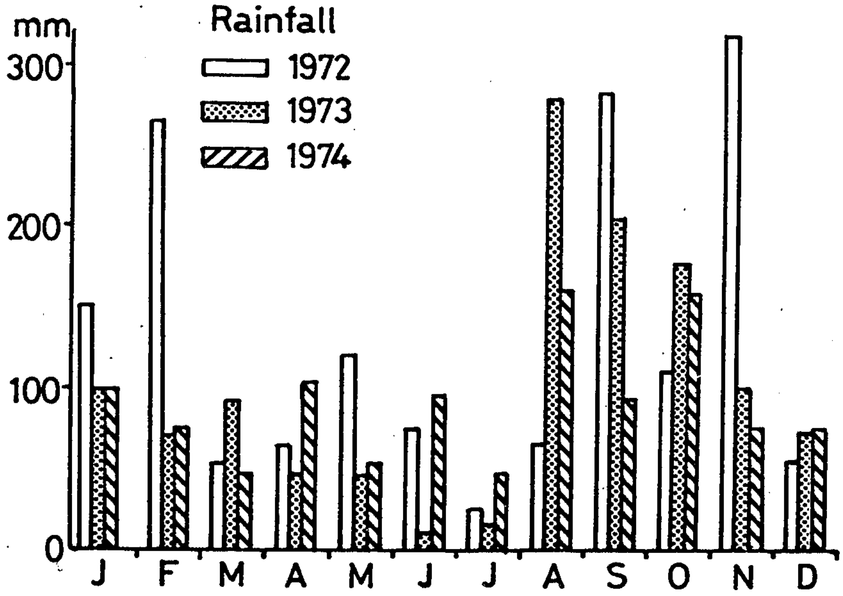

Fig. 20. Rainfalls in Sapporo for three years.

on the other species (Table 21) at UCA. But at UCB, 20 m aprat from UCA, the population was not so large in 1974.

Drosophila nipponica

Fig. 21 shows the results of weekly collections at BG. The appearance of post-hibernation females with undeveloped ovaries starts abruptly from mid May and lasts to late May, and they soon develop their ovaries. In early June the female population abruptly decreases its number and enters a relatively stable phase in completely mature condition, which lasts for about one month till early July, when the emergence of $G_1$ starts. The breeding of $G_h$ was confirmed at five

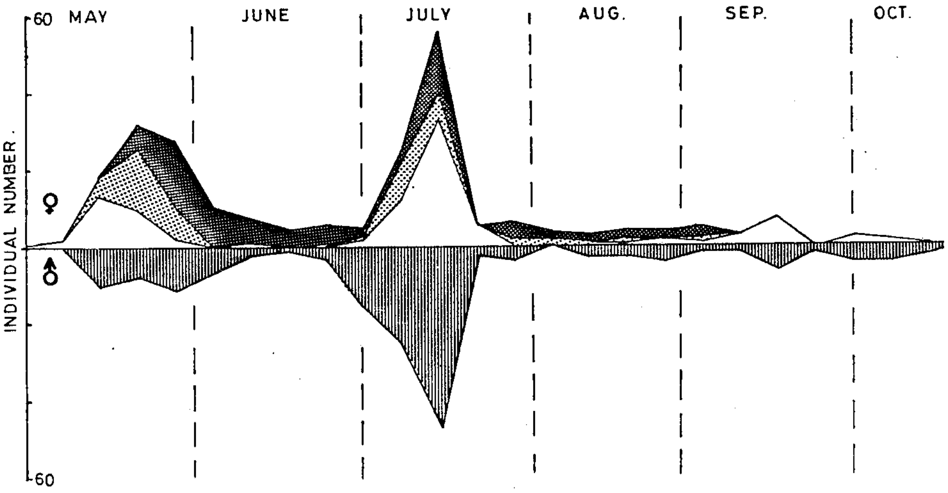

Fig. 21. Seasonal change of female reproductive conditions and male number of D. nipponica in weekly collections in BG

host plants, A. flaccida, H. dulce, A. sylvestris, Osmorhiza aristata, and Lilium cordatum var. glehni, in BG. The emergence of $G_1$ young flies, which begins from early July as mentioned above, bursts forth in mid July, resulting in a conspicuous peak. The newly emerged females soon develop their ovaries. In the late July the individual number of samples drops drastically, and thereafter fluctuates at a very low level till the end of fly season. Against the case of S. pallida, in the present species the cause of such low density in the later half of the season are not known. Although the small number of individuals collected does not allow to follow the sequence of generations accurately, at least the second and the partial third breedings are detectable. Mature females of $G_1$ are found from mid July probably to late August or early September. Their progeny begins to emerge from mid August, and at least a fraction of them is supposed to undergo the third breeding, i.e., a few females emerged before early September develop their ovaries. The remaining majority of $G_2$ emerged in early to mid September, together with few individuals of $G_3$ emerged later, enters the reproductive diapause, without developing their ovaries. Then this species passes through mainly two, but partially three, generations per year.

Drosophila collinella, D. tenuicauda, and D. mommai

Fig. 22 shows the seasonal changes of reproductive age structure of three species based on the results of weekly collections in NF. The hibernating generation ($G_h$) of these species appeared in late May, and the peak of population size was observed in early June for these three species, two or three weeks later than S. pallida or D. nipponica in BG. The population in June was occupied almost by ovarially matured females. These $G_1$ flies decreased in June and disappeared by early July. Their seasonal fluctuations were much different after July. $G_1$ young flies of D. collinella begin to emerge in mid July and last to late July. They soon develop their ovaries and seem to breed. The $G_1$ females with matured ovaries seem to survive till

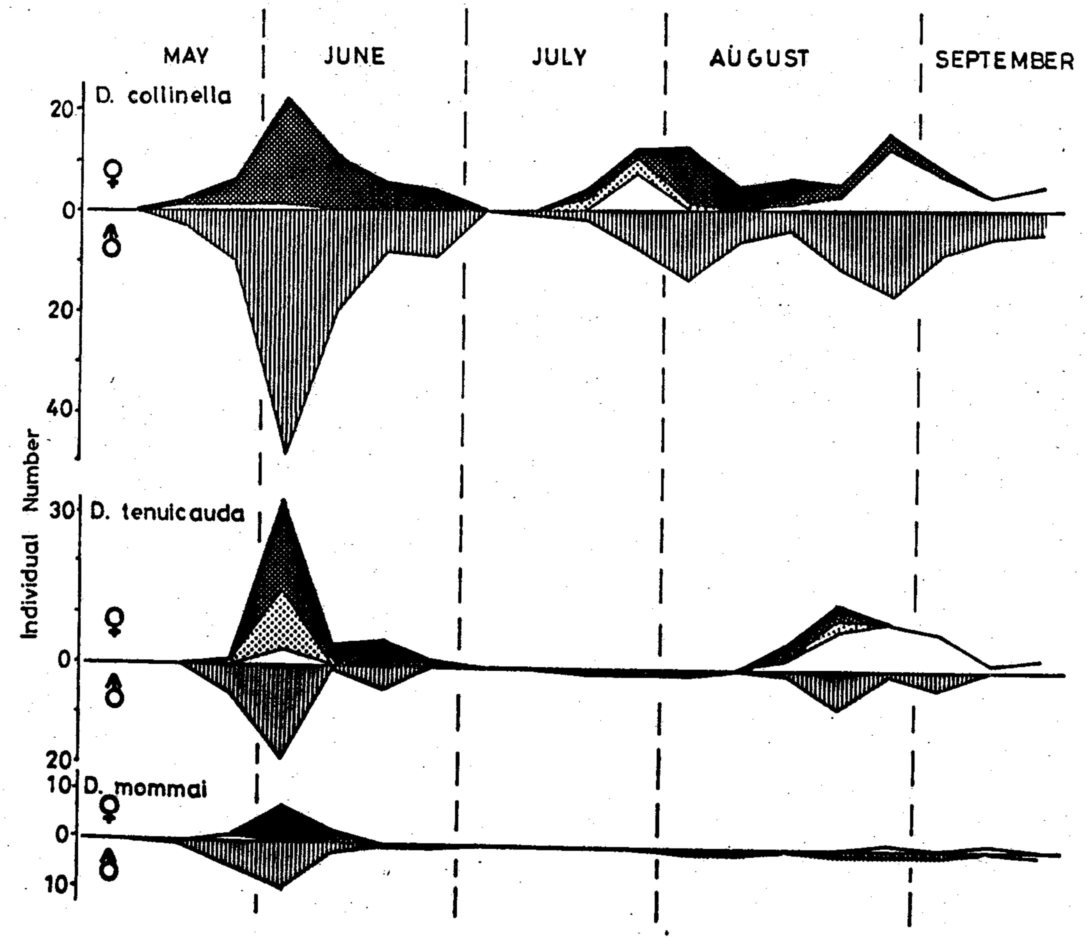

Fig. 22. Seasonal changes of female reproductive conditions and male numbers of *D. collinella*, *D. tenuicauda*, and *D. mommai* in the weekly collections in NF. Legends cf. Fig. 8.

late August or early September. The $G_2$ flies begin to emerge in late August, and they would enter the reproductive diapause without ovarian development.

In contrast, the $G_1$ flies of D. tenuicauda were seldom collected in late July and early August. Only few males were obtained in that period. The females with mature ovaries were collected in mid August, and perhaps they belong to $G_1$. They disappear by late August, one or two weeks earlier than the disappearance of $G_1$ of D. collinella. The $G_2$ flies begin to appear in mid August, and they also enter the reproductive diapause

The specimens of D. mommai were scarcely collected after July, Then alternation of generations of this species can not be detected by this result. But, as referred later, the breeding of this species was observed in June and September, The first breeding would be made by $G_h$, and the latter by $G_1$. In cnclusion, these species passes through almost two generations per year in the Nopporo Natural Forest.

Scaptomyza consimilis, S. polygonia, and D. magnipectinata

Fig. 23 shows seasonal fluctuations of S. consimilis and S. polygonia at UCA and UCB. These species were collected only in spring, and the breeding of the former species was observed only in June. The breeding of S. polygonia was not observed in this survey.

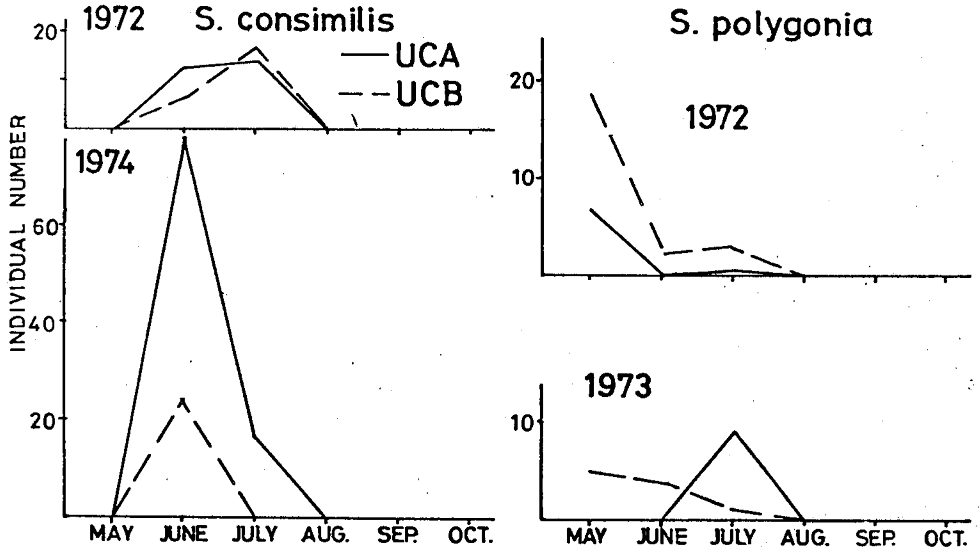

Fig. 23. Seasonal fluctuations of S. consimilis and S. polygonia at UCA and UCB.

The individuals collected in May and June are $G_h$. the appearance of $G_h$ of S. consimilis seems to be somwhat later than S. pallida and S. polygonia. The $G_1$ adults of these species seem to emerge in July, but after July these species were seldom collected by net sweeping on herbage layers. D. magnipectinata was also collected almost in June and July, but negligible thereafter. It was not certain whether the $G_1$ flies of them reproduce or not; they ma be univoltine.

Seasonal life cycle of D. nigromaculata was studied by Watabe et al. (unpubl.). According to them, this species shows a very similar seasonal life cycle with the fungus feeders such as *D. brachynephros*, i.e., this species passes through mainly three, but partially two, generations per year. This species were collected abundantly by sweeping on herbage layer from May to July in BG, but thereafter seldom collected by sweeping. By trap collections using fermenting banana it was collected in considerable number in that season, August and September.

Table 24 shows records of breeding of each species on herbage plants. The breeding of *S. consimilis*, *S. okadai*, and *D. magnipectinata* were observed only in spring, but the breeding of the other species were observed in late August and early September besides in June and May.

The hibernating adults of *D. nipponica* and *D. tenuicauda* were abundantly collected at the cliff shelters along streams in and near Sapporo. *D. nipponica* was also found under fallen leaves covered with snow, and *D. tenuicauda* under withered ferns. *D. nigromaculata* was collected in cliff shelters and tree holes. *S. pallida* was collected among grass stocks before snow fall, but it was not found hitherto in snowy seasons. These individuals usually have undeveloped ovaries and are not inseminated, but a little fraction was occupied by the females with post-mature ovaries.

Table 24. Records of breeding on decayed leaves and stems.

| | May | | June | | July | | Aug. | | Sep. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | E | L | E | L | E | L | E | L | E | L |
| *S. pallida* | | + | + | + | + | + | | + | + | |
| *S. consimilis* | | | + | + | | | | | | |
| *S. okadai* | | + | + | | | | | | | |
| *D. collinella* | | + | + | + | | + | | + | + | |
| *D. mommai* | | | + | | | | | | + | |
| *D. nipponica* | | + | + | + | | | | | + | |
| *D. magnipectinata* | | + | + | + | | | | | | |
| *D. nigromaculata* | | + | + | + | | | | + | + | |
| *D. tenuicauda* | | | + | + | | | | + | + | |

## Discussion

The decayed plants are abundant in spring and early summer because of the fall down of spring ephemeral plants such as *Anemone flaccida*, *A. raddeana* or *Adonis amurensis*, but the decayed plants are scarce in summer. The herbage feeding species, then, seem to be in a difficulty in summer. Especially in isolated groves or windbreaks surrounded by urban or open areas, only few decayed plants were observed in that season, perhaps because of desiccation. *Scaptomyza pallida*, only one species which is able to live and breed in clover patches in open areas, can leave such groves with few foods. Such ability of *S. pallida* supports its dominance in small groves and open areas. On the other hands, *S. pallida* was rare in deep forest where the breeding materials were observed in summer and autumn more frequently than the isolated groves. This species would not adapt to forest environments in Hokkaido. Stalker (1945) also observed that this species was abundant in lightly wooded regions and clover patches, but rare in deeply wooded regions in North America. Nishiharu (1977), however, observed this species was abundant in forest regions and *S. elmoi*, a sibling species of *S. pallida*, was abundant in rural areas near Tokyo. *S. consimilis* and *S. okadai* were also frequent in isolated groves, especially in

UCA and UCB, and rare in deep forests as NF. But these species can not enter to open areas. Before cultivation by human beings began, such open areas or isolated groves would be rare in Hokkaido. Then these species may be very rare in Hokkaido before human activity began and they may expand their distribution according to human activity. On the other hand, species of *Drosophila*, *D. nigromaculata*, *D. nipponica*, *D. magnipectinata*, *D. mommai*, *D. collinella*, and *D. tenuicauda*, would be native herbage feeders in forests of Hokkaido. The first three species were frequent in isolated groves or windbreaks as well as in forests, but the last three were mostly observed in forests.

*Scaptomyza pallida* passes through usually three, but partially two, generations per year in BG, while *D. nipponica* does mainly two, but partially three, generations in the same area. This difference was due to the early start of spring breeding in *S. pallida*, which results in early appearance of $G_1$. The reproductive diapause of *S. pallida* may end earlier. At NF *D. collinella*, *D. tenuicauda*, and *D. mommai* pass mainly two generations per year. In NF, the appearance and peak of $G_h$ populations of these species were later than those of *D. nipponica* in BG. This would be due to the lower temperature in forest of NF; snow thawing was two or three weeks later in NF than in BG. In summer *D. tenuicauda* and *D. mommai* were scarcely found on herbage layer, but *D. collinella* was found frequently in summer. The former two species may pass summer in aestival diapause, as the breeding materials were rare in that season. *S. consimilis*, *S. polygonia*, and *D. magnipecitnata* were seldom found after July, and no breeding was observed in that period. These species may be univoltine; they may pass summer, autumn, and winter in diapause.

As reported in Part III, fungus feeders usually pass through two or three generations per year in NF or in other forest areas. The appearance of $G_h$ and $G_1$ of them was not different from that of *D. nipponica* in BG. After $G_1$ the seasonal life cycle of fungus feeders and herbage feeders was different; fungus feeders seem to pass one or two generation thereafter, but herbage feeders do only one. This difference would be owing to the difference of the abundance of breeding materials in summer and autumn. Fungi were rather abundant in that season, but herbage plants seldom decay. The shortage of materials for breeding has deep influence in their seasonal life cycles.

Tauber and Tauber (1969, 1972, 1973a, 1973b, 1975, 1976a 1976b) also observed that seasonal life cycles of some *Chrysopa* species were influenced by food conditions in the areas they lived. *Chrysopa carnea carnea* which dwells in rural areas in the East

Coast of North America, is a multivoltine, but *C. carnea mohave* which occurs in the rural areas in California where its foods are scarce in summer, enter the aestival diapause in response to the food conditions. *C. downesii* which dwells in coniferous forests in the East Coast, breeds only in spring. They assumed that the univoltinism of this species evolved as the foods were scarce in summer and autumn in coniferous forests.

The herbage feeders have very similar preferences for plants as shown in Part I. It is of interest how they coexist, and why they did not specialize to some kinds of plants. MacArthur and Wilson (1967) proposed the concept of r- and K-selection and Pianka (1970, 1972) clarified the characteristics of r- and K-selected organisms. According to them species which suffer with catastrophic and non-directed mortality have greater r, and intra- and interspecific competition among them are often lax. As referred previously, the population size of herbage feeding drosophilids was affected considerably by rainfall, and the population size fluctuates seasonally and yearly very much. It seems to be also true for fungus feeders; the abundance of fungi was controlled by the rainfall, and moreover, the decay of the fungi was also influenced by rainfall or moisture. These catastrophic and non-directed mortality by rainfall lead the drosophilid flies to r-strategist, and may weaken the competitive ability of them. This may result in coexistence of them.

Emlen (1973) considered that where animal numbers are held down by predation or physical environmental factors, food is by definition, more plentiful, and food specialization is more likely, and where animal populations are prevented from further increase by available food, then by difinition, food is scarce and specialization is a luxury that can not be afforded. In the case of herbage feeding drosophilids, the populaions seem to be controlled by physical factors such as rainfall, but through food conditions. The food is, then, a direct limiting factor of population size in a period with scarce rainfall, and then food specialization may be prevented. Moreover, a special kind of plants did not go to decay through whole seasons, but it has own periods of growing and falling as referred previously. Then drosophilid species must feed and breed on different plants in different seasons. Such seasonal heterogeneity of food conditions also seems to prevent the food specialization.

## Concluding Remarks

The changes of food preference were observed in the members of the *immigrans*-*Hirtodrosophila* radiation, from saprophagous species to species which prefer fresh fungi. The original fungus feeders were saprophagous, such as *D. testacea* or *D. brachynephros*, and they are rather generalists. *D. confusa* and *D. alboralis* seemed to be attracted to fresh fungi as well as decayed ones, and they specialized their fungus preferences to some extent. *D. sexvittata* shows a clear preference for fresh fungi, and it specializes somewhat to the fungi of Tricholomataceae, though it breeds on various fungi. Among the species studied, *D. trivittata* has the most intense preference for fresh fungi, and also has the narrowest preference for fungi of Tricholomataceae. The last two species also seemed to change their ovipositing habit in the course of specialization to fresh fungi.

There was assumed that the inter- and intraspecific competition, overall food abundance, and nutritive conditions of foods were as possible factors which bring the evolution of food preference in fungus feeding *Drosophila*, The role of inter- or intraspecific competition in evolution of food preference was discussed frequently. A dietary separation is considered as one of factors which allow the coexistence of species, and its examples were shown repeatedly. For example, Reynoldson and Davis (1970) observed four triclads which occur together have different food preferences, and Kohn (1959) also observed that several sympatric congeneric species of marine snail genus *Conus*, eat distinctly different foods. This dietary separation is assumed to be established in the course of the interspecific competition. The phenomenon of "character displacements" which refers to increased differences between species when they occur together, is also evidence that competition changes the food habits. In fungus feeding *Drosophila*, the specialization of *D. trivittata* to the genus *Pleurotus*, and the avoidance of *D. sexvittata* and *D. alboralis* from this genus would be partly due to their competition. In addition, the frequent use of fungus stipes for breeding by *D. alboralis* may be a result of interspecific competition with *D. sexvittata* which breeds on caps of fungi mainly.

The importance of food abundance in food specialization of animals was emphasized by Emlen (1973), and he thought that the narrow host selection of phytophagous insects is due to the abundance of host plants. In addition, when a species specializes to a kind of food, it is an ideal that this food is abundant temporally as well as spatially, otherwise this species must survive by aestivating, hibernating, or migration to favorable place during periods with scarce food, and this may decrease the advantage to specialize. The specialization of *D. trivittata* to the fungi of *Pleurotus* was partly due to the overall abundance of the fungi of this genus.

Nutrient factors also have important effects on food preferences. Each species has limited ingestive ability, and can not feed on every thing~~s~~. In the course, of evolution of food habits, animals put a new type of food into their menue, and at the same time they may lose a food of old type. *D. trivittata* and *D. sexvittata* became to feed on fresh fungi and at the same time they lost a ability to feed on decayed fungi. Though they have specialized to the fresh mushrooms, they did not get the ability to feed on every fresh mushrooms; they can not feed on fresh *Agaricus* or *Coprinus*.

Nutrient factors have another important role in the evolution of food preference in animals, coevolution with plants. Individuals of plants must defend their collected energy against all would-be consumers. An attack by a herbivore selects an adaptation of defense in the plants, or even a counter attack. This cycle of attack and counter attck between plants and herbivore leads these organisms into complicate relationships. Plants have developed various defense mechanisms from herbivore. Some chemical by-products in the synthesis of primary metabolic products, such as alkaloids, nicotine, or tannins, are toxic to animals, or at least repellant. But once insect species has evolved a mechanism for tolerating or detoxifing the plant's defense, secondary metabolic products can be utilized by the insect as cues to identify the plant for feeding and breeding. Moreover, this insect has an advantage to maintain its population, because no or few competitors are found on this plant. Nutritional inferio~~l~~rity of plants also acts as a defense mechanism. For example, $C_4$ plant species have most starch stored around the vascular bundles and it is less available to herbivore (see for review, Price, 1975). Fungi of *Agaricus* or *Coprinus* were seldom eaten by drosophilids when fresh. It may be due to the nutritional inferio~~l~~rity of their black spores which are hard to ingest, and these black spores may be evolved in coevolutionary interactions with fungivorous insects. Several mushrooms have toxic chemicals, such as alkaloids, but the adaptive meaning of such chemicals is not known.

In contrast to the food specialization or dietary separation among the members of *Hirtodrosophila* radiation, the members of the *immigrans* radiation did not show a clear separation of fungus preference. Moreover, among the herbage feeders, species of different taxonomic groups, *Scaptomyza*, *Sophophora*, or *Lordiphosa*, use similar plant flora for breeding and they occur together. They may have different preferences for yeasts or bacteria. Further, their coexistence was discussed on the concept of r- and K-selection; r-strategists which are under unpredictable conditions has sometimes weak competitive ability and this may allow the coexistence of species having similar niches. Their food generalization was discussed on temporal heterogeity of food conditions and on population regulation. It is a very rare that one kind of fungi or plant goes to decay through whole seasons, so that they are forced to feed on different foods in different seasons. Further, food is a limiting factor of population increase of drosophilid species in periods with scarce rainfall, because decay or fermentation does not proceed. In such conditions insects can not maintain their populations on only one kind of food, and they tend to use a wide range of foods. Such mechanism of coexistence or food generalization was scarcely known up to present, because most studies centered to find out a difference between species or specialization of food preferences. Further study is needed on these points.

In conclusion, the food preference of drosophilid flies evolved in interactions with various environmental factors, the food abundance, seasonality of foods, nutritive factors of foods, or competitors. Weather or enemies also seem to have influence on food preference through the regulation of population fluctuation.

# Summary

The food preferences, abundance, microdistribution, and seasonal life cycle of drosophilid flies were studied in and near Sapporo, and the evolution of food preferences is discussed in relation to the ecology of the flies and host plants.

1) The breeding sites of drosophilid flies were studied. Four types of substrates: fermenting fruit, slime fluxes, decayed leaves and stems, and fleshy fungi, were used as breeding sites by 42 species of Drosophilidae. Among these sites, fruit was less important for temperate drosophilid flies, because fruiting plants were few and the fruiting season was usually in autumn, after the breeding season of wild drosophilid flies had terminated. Each drosophilid species mainly depended on only one type of breeding sites, though it sometimes used other breeding sites subsidiarily. In the main breeding site, each species used several plant or fungus species or families, which suggests they are polyphagous. Members of the same species group or subgenus generally used the same type of breeding site, but with some exceptions. Further, different groups used the same breeding sites. The genus *Leucophenga*, the genus *Mycodrosophila*, the *funebris* group, the *testacea* group, the *quadrivittata* group, the *melanderi* group, *D. histrio*, and *D. confusa* specialized in fleshy fungi. Most species of the *quinaria* group also preferred

fleshy fungi, but *D. nigromaculata* used the decayed leaves of herbaceous plants as its main breeding site. The genus *Scaptomyza*, the subgenus *Lordiphosa*, the *nipponica* subgroup, *D. mommai*, and *D. tenuicauda* specialized in the decayed leaves or stems of herbaceous plants. The subgenus *Scaptodrosophila*, the *obscura*, *virilis*, and *robusta* groups have adapted to slime fluxes. The *immigrans* group and most of the *melanogaster* group preferred fermenting fruit. The similarity in breeding habits in different groups is considered as the result of parallel evolution. The difference in feeding habits between adults and larvae was observed in members of the *robusta* and *quinaria* groups and in some others.

2) Food preferences of fungus feeders of the *immigrans*-*Hirtodrosophila* radiation were studied in the field and laboratory. There was assumed to be an evolution of feeding habits, from the saprophagous habit to the fresh fungus feeding habits. Further, according to this evolution, a specialization in fungus preference seemed to take place. Adults of *D. nigromaculata*, a herbage feeder, and *D. immigrans*, a fruit feeder, could not get sufficient nutrition for survival and reproduction from mushrooms, and they used limited fungi for feeding and breeding in the field. *D. testacea* and *D. brachynephros* preferred decayed fungi for feeding and breeding, and could reproduce well on the decayed fungi. *D. testacea*,

*D. histrio*, *D. brachynephros*, and *D. unispina* used a wide variety of fungi, and they have very similar fungus preferences to each other. *D. confusa* also resembled to the above four species in feeding habit, but differred from them in some points; it was attracted frequently to fresh *Polyporellus squamosus*, and it preferred the fungi of Aphyllophorales more than the above species. *D. alboralis* was attracted to fresh mushrooms to some extents. This species was unique in its frequent use of the stipes of fungi as larval breeding sites. Adults of *D. sexvittata* and *D. trivittata* had a strong preference for fresh fungi, but their larvae preferred decayed fungi like the above species. The former species used a wide variety of fungus species, though it showed some preference for Tricholomataceae. But the latter had a strong preference for Tricholomataceae, especially for the fungi of *Pleurotus*. Inter- and intraspecific competition were considered as possible factors which had drivied *D. sexvittata* and *D. trivittata* to prefer fresh mushrooms. These two species seemed to avoid the fungi of *Agaricus*, *Coprinus*, and Boletaceae, because these fungi are innutritive to drosophilid flies when fresh. These species were also characterized by the use of lamellae as oviposition sites and their eggs without filaments. The other species oviposited into the upper surface of the cap and stipes, and their eggs have a few filaments. *D. quadrivittata* and the members of *Mycodrosophila* seemed to prefer the fungi of Aphyllophorales.

3) The abundance, microdistribution, and seasonal life cycle of fungus feeding drosophilids were studied in and near Sapporo. In the members of the *Hirtodrosophila* radiation, *D. trivittata* and *D. sexvittata* were collected abundantly, and in the members of the *immigrans* radiation, *D. testacea*, *D. brachynephros*, *D. unispina* and *D. confusa*, were frequent. The number of species of the *Hirtodrosophila* radiation in an area increased with an increase in the number of fungus species and the amount of fungi in that area. But the number of species of the *immigrans* radiation was rather stable irrespective of number of fungi us species ? or the amount of fungi. *D. testacea*, *D. brachynephros*, and *D. sexvittata* were found frequently in isolated groves or windbreaks. Their broad fungus preferences, great migratory ability and/or habitat preferences for open areas seemed to allow them to maintain populations in a small groves. Most fungus feeders were reproductively active from late May to early September, and during this period they passed through two or three generations. They pass winter as adults in the reproductive diapause. Seasonal change in their host fungi were studied in relation to the seasonality of the fungi. The specialization of *D. trivittata* in the fungi of *Pleurotus* was assumed to be enforced by the spatial and temporal ubiquity of these fungi, and the

avoidance by *D. sexvittata* and *D. alboralis* of these fungi was considered to be the results of interspecific competition with *D. trivittata*.

4) The abundance, microdistribution, and seasonal life cycle of herbage feeding drosophilids were studied by sweeping collections in and near Sapporo. The individuals obtained by sweeping on the herbage layer generally belonged to the herbage feeders, which breed on the decayed leaves and stems. *S. pallida* was dominant in isolated groves and in clover patches in open areas. *S. consimilis* and *S. polygonia* were generally found in isolated groves. *D. mommai*, *D. tenuicauda*, and *D. collinella* were frequent in forests but scarce in isolated groves, but *D. nipponica* *D. magnipectinata*, and *D. nigromaculata* were frequent in both forests and isolated groves. *S. pallida* passes through mainly three, but partially two generations per year. The breeding of its post-hibernating generation was done mainly on decayed leaves of spring ephemeral plants in isolated groves, but the individuals of the first generation seemed to leave the groves for clover patches in open areas, and performed their breeding there. *D. nipponica*, *D. collinella*, *D. tenuicauda*, and *D. mommai* pass through mainly two generations per year. The last two species were seldom collected in summer when decayed leaves were scarce, and they may be in aestival diapause in that season. Specimens of *S. consimilis*, *S. polygonia*, and

*D. magnipectinata* were collected frequently from May to July, but seldom thereafter. They may be univoltine. The influence of the scarcity of food on the seasonal life cycle of the flies is discussed. The population size of herbage feeders fluctuated seasonally and yearly. Rainfall during the larval growing periods is considered as a cause of fluctuation, because the decay of plants did not proceed in seasons or years with low rainfall. The coexistence, overlap of food niches, and food preferences of drosophilid flies are discussed on the basis of the ecology of the flies and food plants.

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