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# Daily Activity and Vertical Microdistribution of Drosophilid Flies in Undergrowth Layers

By

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(With 6 Text-figures and 3 Tables)

The recent advances of drosophilid population genetics have revealed the necessity of detailed ecological information taken under natural conditions to understand the population behaviour precisely. Among various aspects explored for such necessity, for instance, geographical distribution, feeding habits, seasonal activity, etc., the daily activity has called special attentions of many workers (Dobzhansky and Epling 1944, Pavan *et al.* 1950, Taylor and Kalmus 1954, Ishihara 1955a, b, Dyson-Hudson 1956, Nozawa 1956, Wakahama 1957, Wakahama *et al.* 1963, Lee 1962, Kaneko 1968, etc.). These studies have clarified a bimodal crepuscular activity peculiar to most drosophilid flies. Although such data are not yet appropriately incorporated in the studies of population genetics, Mitchell and Epling (1951) made a preliminary discussion on the mechanism of genetic differentiation based upon the different daily activities according to vegetation types. To promote a balanced advance of the analysis of drosophilid populations, the results of population genetics studies must reciprocally be incorporated in ecological studies of local drosophilid assemblages.

As to the distribution of insects above the ground surface, numerous studies have been made on the so-called "aeroplankton" found up to considerable heights (for instance, 15,000 feet, Glick 1939), using aeroplanes or balloons (cf. Johnson 1969). But the distribution in relation to vertical plant stratification, being conspicuous in the course of plant succession mainly depending on light requirement, has so far relatively been ignored, with the exception of several studies on disease vector mosquitoes. While most aeroplankton are passively carried out by air current, the vertical microdistribution related to plant stratification involves active responses of animals to the environment, for instance, feeding and breeding habits, adaptability to some external factors, etc. Concerning drosophilid flies Greuter (1963) observed the distribution of *D. subobscura* and *D. obscura* up to the forest canopy and Krizelj (1968) found many drosophilid flies from the canopy in his sampling of dipterans at various vegetations and heights.

In the present study daily activities of drosophilid flies were surveyed at different heights in undergrowth layers of forest and grassland, adopting the usual trapping method with fermented banana.

Before going further, the author should like to define the activity studied as "the flight in search of food which leads the flies to enter traps" (Dobzhansky and Epling 1944). More precisely explained, "the variations in number of flies caught throughout the day reflects a difference in *Drosophila* activity (and not a difference in the attraction radius of the bait, possibly caused by changes in environmental conditions), for collections of *D. subobscura* made by suction traps (Taylor and Kalmus 1953) showed similar pattern of variation in numbers of flies caught throughout the day to that which he found in his collections of the same species, using bait" (Dyson-Hudson 1956).

The collection at different heights, adopting the method depending on the feeding activity, may serve to give a general perspective of distribution as a first approximation to know the vertical range of flight, though Johnson (1969) points out distortions of natural vertical distribution by using light or bait traps.

### Collecting method

The area studied is located within Misumai Arboretum of Hokkaido University in the suburb of Sapporo City. Ecological and topographical conditions of the area were described previously (Toda 1973). Two trap stations were chosen in two different vegetations; one in natural forest (NFa, T.st.I) and the other in grassland (GA, T.st.IV). At each trap station four trap tins with banana pieces fermented by Baker's yeast were set at four different heights (20, 50, 100, 150 cm h.). Each tin was set 2~5 m apart from each other in order to avoid the entry of flies coming to other traps at sampling (Fig. 1).

Collections were made in different weathers and seasons in 1971; on June 8, 10, 12, 14, August 11, 13, 15, 17, and October 8, 9, 14, 16. The baits were not changed for two successive collecting days in the same month. Recording of air temperature and relative humidity was carried out at each different height of both stations for four days each in June, August and October (June 9, 11, 13, 15, August 12, 14, 16, 18 and October 8, 10, 15, 17), by using an Assman's psychrometer, together with estimation of general weather and wind class by eye. The trap stations were visited for collections and climatic observations every 2 hr., 8 times from 5:00 to 19:00 in June, 7 times from 5:00 to 17:00 in August and 6 times from 7:00 to 17:00 in October. The heights of main undergrowth plants at both trap stations were recorded occasionally from May to October.

### Results and discussion

The results are divided into two parts, the first part dealing with each species separately while the second part analysing the drosophilid assemblage of the area studied as a whole.

1. *Daily activity and vertical microdistribution of predominant species*: Daily activity patterns of many species inhabiting Hokkaido or other localities have been reported by several authors. In this section daily activity and vertical micro-

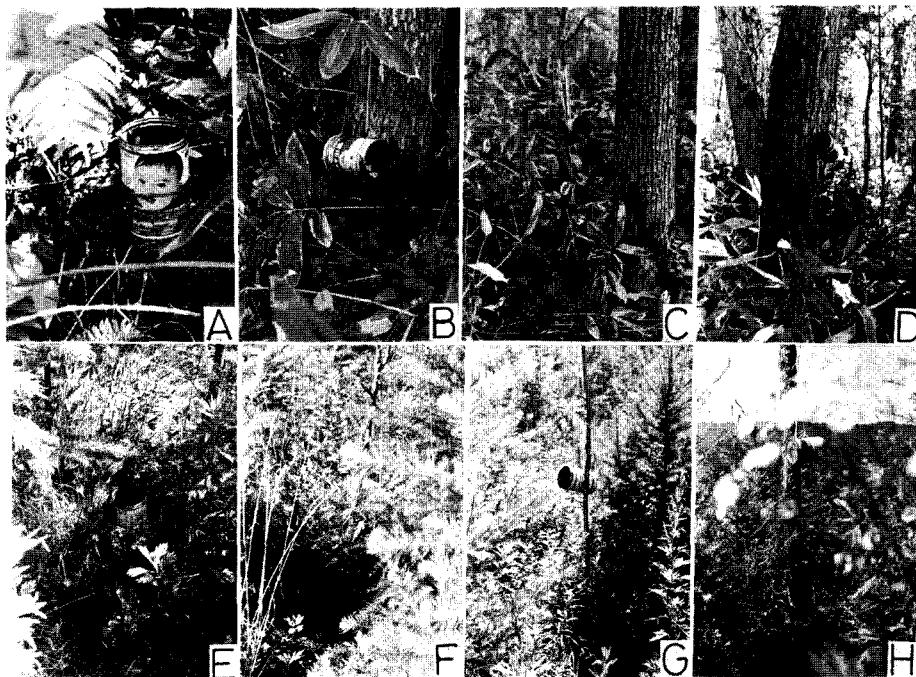


Fig. 1. Trap tins at trap stations. A, 20 cm h. B, 50 cm h. C, 100 cm h. D, 150 cm h. in forest, E, 20 cm h. F, 50 cm h. G, 100 cm h. H, 150 cm h. in grassland.

distribution of twelve species predominant in the present study are described, in connection with seasons, weather conditions, heights from the ground and vegetations. The results presented in Fig. 2 show typical cases as well as some abnormal ones but the patterns described below are more or less common to other instances not illustrated.

a) *D. confusa* (Fig. 2-A<sub>1-4</sub>): This species was collected abundantly in forest in spring (cf. Toda 1973). The daily activity showed a typical bimodality with a higher peak in morning and a lower one in evening on fine days in June (A<sub>1</sub>), while a unimodal tendency with a morning peak in August (A<sub>3,4</sub>). On cloudy and rainy days, the periodicity was not clear (A<sub>2</sub>). In contrast to the clear bimodal periodicity at higher traps, morning and evening peaks were less conspicuous and flies were also collected sporadically in midday at lower traps. The vertical distribution pattern was stable in forest throughout season and daytime, always significantly more abundant at two higher traps.

b) *D. coracina* (Fig. 2-B<sub>1,2</sub>): Forest species. A peculiar unimodal activity with the midday peak was observed in June and August as recorded by several

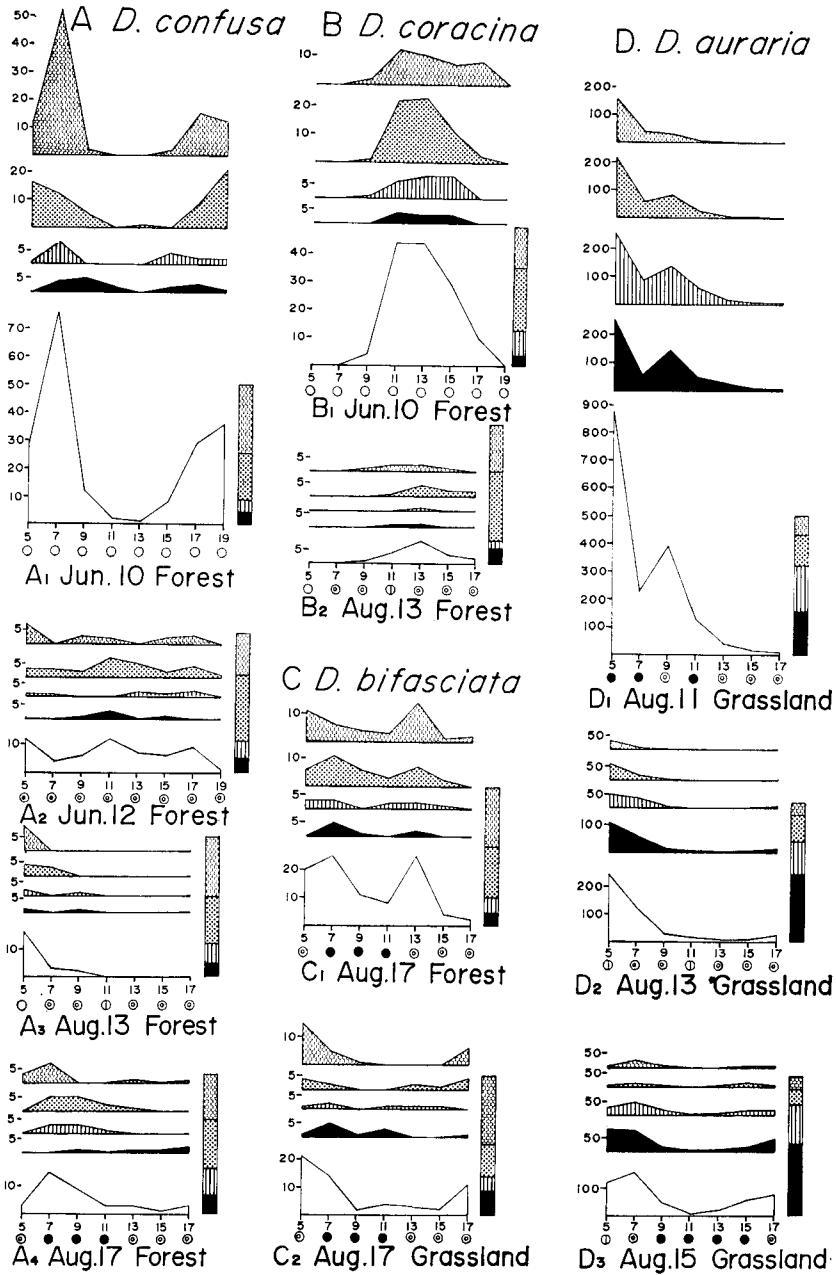
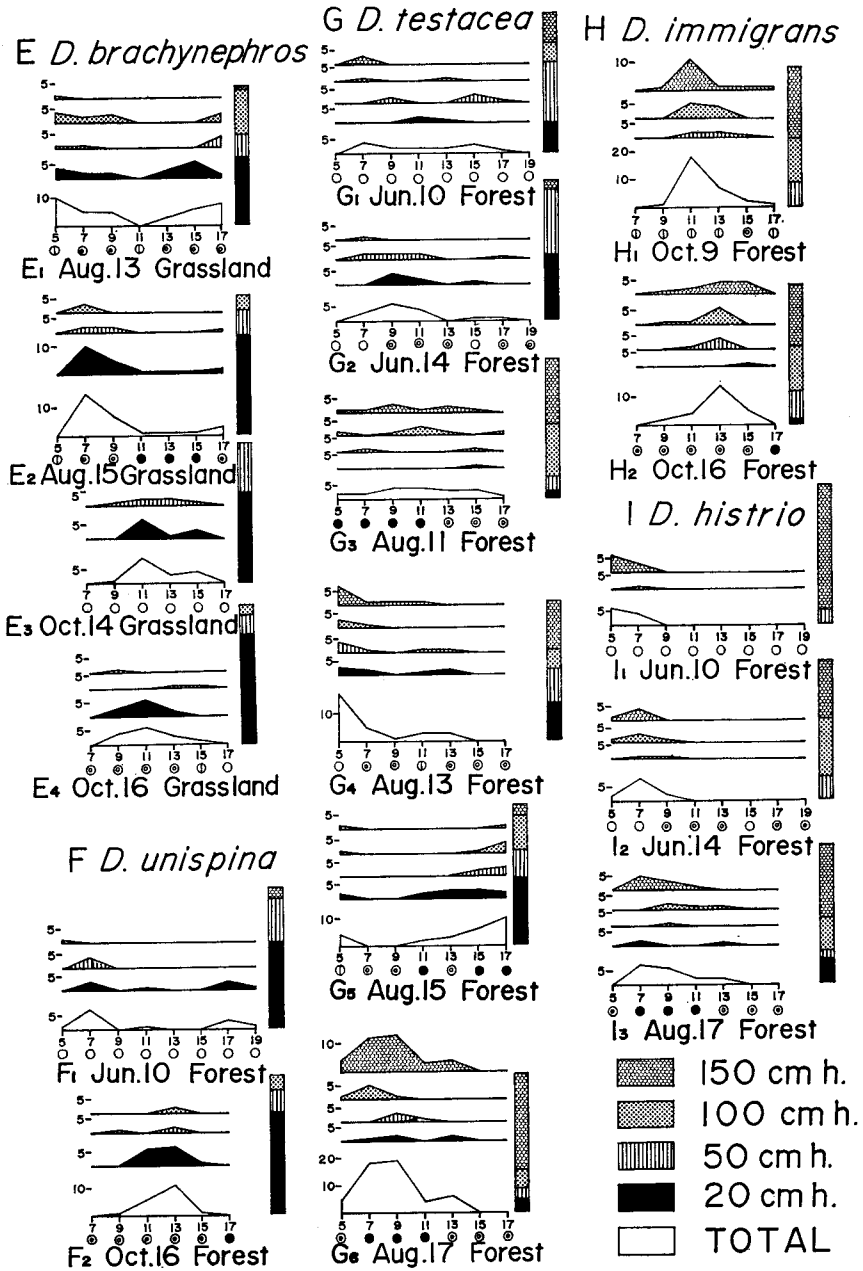


Fig. 2. Daily activity and vertical distribution of predominant species, given separately (●, rainy) at bottom. Right histograms show percentage ratios of specimens collected at



rately for each vertical height, general weather conditions (○, very fine ◐, ⊙, cloudy various heights.

authors in Hokkaido (Shima 1960, Kaneko 1968). The activity was apparently depressed down on cloudy and rainy days. Many specimens (141 and 82) were collected on fine days (June 10 and 14, respectively), while few on cloudy days (June 8 and 12, respectively 21 and 1). The same tendency was observed in August, too. This species was more abundant at higher traps, especially at 100 cm h.

c) *D. bifasciata* (Fig. 2-C<sub>1,2</sub>): The daily activity pattern differed between forest and grassland. While a typical bimodal activity with a higher morning peak and a lower evening one was observed in grassland (C<sub>2</sub>), the later peak appeared at 13:00 in forest (C<sub>1</sub>), distinctly earlier than the evening peak in grassland obtained on the same day, and than the usual evening peak so far recorded in Hokkaido (Ishihara 1955, etc.). In grassland, the periodicity was less distinct at lower traps like as in *D. confusa*. This species was significantly abundant at two higher traps in forest and, though less conspicuous, in grassland, too.

d) *D. auraria* (reported previously as *Drosophila auraria* A, cf. Kurokawa 1952) (Fig. 2-D<sub>1-3</sub>): This species was very abundant in grassland in August (cf. Toda 1973). Bimodal activity with a higher morning peak and a lower evening one is recognized as a general tendency, nevertheless daily activity patterns varied from day to day, apparently in part affected by adverse weathers. Although bimodality was observed on August 13 and 15 (D<sub>2,3</sub>), only the morning activity was very high on August 11, with two peaks at 5:00 and 9:00 (D<sub>1</sub>), and a clear periodicity was not observed on August 17. Such deviations from bimodal pattern due to climatic and topographic conditions have been reported by many authors in this species (Makino *et al.* 1954, Nozawa 1956, Wakahama 1957, Wakahama *et al.* 1963, Lee 1962, Kaneko 1968).

This species was significantly abundant at two lowest traps in grassland. Although being a typical grassland species, some specimens were collected in forest on August 11, when a very high activity was observed in grassland. It is noticeable that distribution of these forest specimens was reverse to that of grassland ones, being significantly more abundant at higher traps (0.0, 6.2, 12.5, 81.3% at 20, 50, 100, 150 cm h., respectively).

e) *D. biauraria* (reported previously as *Drosophila auraria* B, cf. Kurokawa 1952): The vertical distribution of this species differed between forest and grassland as in *D. auraria*: significantly abundant at two highest traps (2.6, 7.7, 41.0, 48.7% at 20, 50, 100, 150 cm h., respectively) in forest, while more abundant at lower traps (45.4, 27.3, 21.2, 6.1% at 20, 50, 100, 150 cm h., respectively) in grassland. The daily periodicity was not clear.

f) *D. brachynephros* (Fig. 2-E<sub>1-4</sub>): This grassland species showed a weak bimodal activity in August (E<sub>1,2</sub>). In October separation of two peaks became obscure (E<sub>3</sub>) or even disappeared (E<sub>4</sub>). This species was significantly abundant at two lowest traps.

g) *D. unispina* (Fig. 2-F<sub>1,2</sub>): The daily activity of this forest species showed a bimodality with a higher morning peak in June (F<sub>1</sub>), but a unimodality with

a midday peak in October ( $F_2$ ). This species was significantly abundant at two lowest traps like as *D. brachynephros*.

h) *D. testacea* (Fig. 2- $G_{1-6}$ ): This species was collected frequently in forest in June and August. Both daily activity pattern and vertical distribution fluctuated day by day.

i) *D. immigrans* (Fig. 2- $H_{1,2}$ ): Although the bimodality was reported by several authors (Pavan *et al.* 1950, Ishihara 1955) for this forest species, in the present study a unimodal activity with a midday peak was observed in October ( $H_{1,2}$ ). The vertical distribution showed an upward increasing gradient.

j) *D. histrio* (Fig. 2- $I_{1-3}$ ): Forest species. The daily activity on fine day showed a unimodality with a morning peak in June and August ( $I_{1-3}$ ), though the prolonged active phase and delayed peak were observed in adverse weather ( $I_3$ ). The vertical distribution showed an upward increase like in many other forest species.

k) Other species

*D. imaii* collected in forest in August showed an apparent vertical microdistribution gradient, significantly abundant at two highest traps (4.5, 4.5, 36.4, 54.6% at 20, 50, 100, 150 cm h., respectively). *D. sordidula* was relatively frequent in forest in June and August, generally showing bimodal daily pattern and upward increase in vertical distribution.

*Discussion:* From the studies on *D. pseudoobscura* in California, Dobzhansky and Epling (1944) presented a hypothesis that "light is the principal causal factor which determines the diurnal periodicity". Lilleland (1938) showed experimentally that in the absence of food the life span of *D. pseudoobscura* and *D. persimilis* is greater at higher humidities; 38~53 hours at 0% R.H. and 57~93 at 95% R.H. (both at 24°C). Pavan *et al.* (1950) and Mitchell and Epling (1951) described that water loss is a great hazard to which drosophilid flies are exposed in nature, concluding the crepuscular activity controlled by light intensity as a behavioural adaptation to avoid desiccation. Furthermore, Taylor and Kalmus (1954) proposed an interesting hypothesis that drosophilid flies may have become adapted to increased intense daytime aridity not through increased resistance to desiccation, as in most other Schizophora, but through increasing visual efficiency to low light intensities, combined with a shift of flight periodicity to darker and climatically less severe period.

In the present study, most species exhibited the bimodal activity or at least a tendency to such with morning and evening peaks (Table 1), which does not contradict the hypothesis by Taylor and Kalmus. The exception is *D. coracina* which showed the unimodal pattern with a midday peak. The species-specificity of the pattern demonstrated by *D. coracina* seems indubitable by the accordance with other records (Shima 1960, Kaneko 1968) and the decreased activity on cloudy and rainy days. The last observation suggests the difference in tolerance zones of this species from other species, higher in temperature and lower in humidity. If the hypothesis by Taylor and Kalmus is valid in general, *D. coracina*



Table 1. Daily activity pattern of predominant species, separately shown for each collecting means (obscure activity) U, unimodal midday activity uc, unclear periphery or cloudy c, cloudy

Vegetation	Forest									
	Date	8	10	12	14	Aug. 11	13	15	17	
General Weather	Jun.	fc	ff	c	fc	cr	c	cr	cr	
<i>D. histrio</i>		—	M	—	M	—	—	—	m	
<i>D. auraria</i>		—	—	—	—	uc	—	—	—	
<i>D. bifasciata</i>		—	—	—	—	—	—	—	uc	
<i>D. soráidula</i>		—	uc	—	—	uc	Me	me	uc	
<i>D. confusa</i>		mE	ME	uc	ME	—	M	—	M	
<i>D. testacea</i>		—	uc	—	me	uc	M	mE	M	
<i>D. brachynephros</i>		—	—	—	—	—	—	—	—	
<i>D. unispina</i>		—	me	—	—	—	—	—	—	
<i>D. immigrans</i>		—	—	—	—	—	—	—	—	
<i>D. coracina</i>		—	U	—	U	—	U	—	—	

may present an interesting exception, showing adaptation to daytime aridity by an increased resistance to desiccation, which caused the midday peak, though conclusive evidence must be obtained through laboratory experiments. This specific activity pattern may have a certain interspecific significance because feeding sites of fermented banana are nearly monopolized by *D. coracina* at or near midday on fine days. This species is distributed widely from Hokkaido to Kyushu and recorded from Korea and China, too. It has yet not been clarified whether the specific activity pattern of this species in Hokkaido is stable in other areas or not, though slight local variations were observed at two localities: evening peak in Anjo, Aichi Prefecture (Nozawa 1956) and abundance in afternoon in Korea (Lee 1962). Unfortunately, daily activities of numerous tropical or subtropical relatives of this species belonging to the same subgenus *Scaptodrosophila* have never been reported.

As mentioned above, most authors considered light intensity as the main factor controlling daily activity. But Dayson-Hudson (1956) pointed out seasonal change of the relative importance of controlling factors from the observation of different patterns of *D. subobscura* between summer and early spring or late autumn, concluding, "In summer, the pattern of activity is determined by light and temperature has a secondary influence. In contrast to summer activity, the activity pattern found in early spring and late autumn appears to be determined primarily by temperature and light has only a subsidiary effect".

In the present study, too, such seasonal change of daily patterns was observed in *D. brachynephros*, *D. unispina* and probably *D. immigrans*. Compared with the patterns in June or August, those in October were characterized by shorter active period, accompanied with the weaker differentiation of two peaks or their final fusion. Such pattern observed in October seems mainly caused by tempera-

day. Activity pattern; M, morning activity E, evening activity (each small letter odicity -, very scarce. General weather condition; ff, very fine f, fine fc, cr, cloudy or rainy.

					Grassland									
Oct.	8	9	14	16	Aug.	11	13	15	17	Oct.	8	9	14	16
	f	f	ff	c		er	c	er	er		f	f	ff	c
	-	-	-	-		-	-	-	-		-	-	-	-
	-	-	-	-		M	Me	Me	uc		-	-	-	-
	-	-	-	-		-	-	-	Me		-	-	-	-
	-	-	-	-		-	-	-	-		-	-	-	-
	-	-	-	-		-	-	-	-		-	-	-	-
	-	-	-	-		-	-	-	-		-	-	-	-
	-	-	-	-		-	me	Me	uc		-	me	me	U
	-	-	uc	U		-	-	-	-		-	-	-	-
	uc	U	-	U		-	-	-	-		-	-	-	-
	-	-	-	-		-	-	-	-		-	-	-	-

ture, which rises above 10°C (the lower limit for flight activity of drosophilid flies) only at midday in October, though the possible influence of light conditions is not excluded.

The weaker differentiation of two peaks and their final fusion in autumn was observed in the total drosophilid assemblages in Botanical Garden and the campus of Hokkaido University by Ishihara (1955) and in *D. nigromaculata* in Botanical Garden of Hokkaido University by Wakahama (1957), who assumed seasonal change of daylight period and temperature as the factors realizing such pattern.

As for other species, they were not collected enough to compare the autumn change of daily patterns in October. Moreover, remarkable change of daily patterns between June and August was not observed in any species, which may be due to relatively similar environmental conditions between June and August.

To test the hypothesis of behavioural adaptation mentioned above, Pavan *et al.* (1950) compared daily activities of humid tropic Brazilian species to *D. pseudoobscura*, distributed in arid to semiarid regions of the Western Hemisphere. It was revealed that most humid tropic species showed remarkable plasticity, by changing the daily activity pattern according to weather conditions during daytime and localities, in contrast to the relatively fixed periodicity of *D. pseudoobscura*.

In the present study, daily activity pattern of most species showed the relatively high plasticity, depending on height, weather, season and vegetation as in Brazilian humid tropic species as summarized in Table 2.

Beyond wide geographic and climatic differences, both humid tropic Brazil and Japan are common in high humidity. Since the species both in the present study and in Pavan *et al.* live in humid area, the danger to desiccation seems not excessive. Under such habitats with mild fluctuation of environmental conditions, only behavioural adaptation may be sufficient to maintain the survival. At the

Table 2. Plasticity of daily activity pattern for various environmental factors.  
 + plastic, - stable, ± undecided, / absence of reliable data.

	Vegetation	Height	Weather	Season
<i>D. confusa</i>	/	+	+	+
<i>D. bifasciata</i>	+	+	/	/
<i>D. biauraria</i>	+	+	/	/
<i>D. brachynephros</i>	/	±	+	+
<i>D. testacea</i>	/	+	+	±
<i>D. unispina</i>	/	±	±	+
<i>D. sordidula</i>	/	±	+	±
<i>D. auraria</i>	±	-	+	/
<i>D. coracina</i>	/	-	+	/
<i>D. histrio</i>	/	±	±	±
<i>D. imaii</i>	/	±	/	/
<i>D. immigrans</i>	/	-	-	/

same time, however, this logically suggests the possibilities of two other adaptive types: Species acquired physiological resistance to desiccation (exception from the hypothesis by Taylor and Kalmus) probably more frequent at arid zones, and those without even behavioural adaptation, which may results in an extreme stenotopy in constantly humid environments such as rain forests and riverside areas.

Table 3. Vertical microdistribution gradient in undergrowth layer of forest and

$$g = \sum_{i=1}^3 \frac{f_{i+1} - f_i}{h_{i+1} - h_i} \quad (-100/30 = -3.333 < g \leq 100/50 = 2.000)$$

Date General Weather	Jun. 8 fc	Jun. 10 ff	Jun. 12 c	Jun. 14 fc	Aug. 11 cr
<b>Forest</b>					
<i>D. confusa</i>	0.632	0.808	0.410	0.575	
<i>D. coracina</i>		0.577		0.523	
<i>D. immigrans</i>					
<i>D. histrio</i>		1.933		1.055	
<i>D. sordidula</i>		1.000			1.179
<i>D. testacea</i>		0.287		-0.802	0.911
<i>D. unispina</i>		-1.485			
<i>D. imaii</i>					
<i>D. bifasciata</i>					
<i>D. biauraria</i>					0.990
<i>D. brachynephros</i>					
<i>D. auraria</i>					1.709
<b>Grassland</b>					
<i>D. bifasciata</i>					
<i>D. biauraria</i>					-1.027
<i>D. brachynephros</i>					
<i>D. auraria</i>					-0.341

The constant gradient in vertical distribution was observed in most predominant species except *D. testacea*, as summarized in Table 3. In general, the direction was reverse between forest and grassland species, upward in the former (*D. confusa*, *D. coracina*, *D. immigrans*, *D. histrio* and *D. sordidula*), while downward in the latter (*D. auraria*, *D. brachynephros*).

As to the relative importance of factors determining distribution pattern, it is important to compare the pattern of the species collected in both vegetations. Among four species collected enough in both vegetations, the gradient was reversed in *D. auraria* and *D. bauraria*, but unchanged in *D. brachynephros* (downward) and *D. bifasciata* (upward).

Interestingly the gradient in forest changed in *D. auraria* but not in *D. brachynephros*, nevertheless both showed similar habitat preference and downward gradient in grassland. Such difference would not be expected if the relative importance of the factors concerned is the same between the two species. It is plausible that the response to each factor is respectively different between two species, probably based upon the genetic differences involved. A set of factors may release the same ultimate responses in grassland but not in forest. The same explanation could be applied to the relation between *D. auraria* and *D. bifasciata*. Concerning close relatives of these species, *D. bauraria* behaved like as its sibling relative, *D. auraria*, and *D. unispina*, a close relative of *D. brachynephros*, showed

grassland. Gradient is separately shown for each collecting day by index *g*.

In the formula  $f_i$  = percentage ratio of specimens collected at  $h_i$ ,

( $h_1, h_2, h_3, h_4$  = 20, 50, 100, 150 cm h., respectively).

U, upward gradient D, downward gradient.

Aug. 13 c	Aug. 15 cr	Aug. 17 cr	Oct. 8 f	Oct. 9 f	Oct. 14 ff	Oct. 16 c	mean g	DG
0.732		0.451					0.601	U
0.737							0.612	U
			0.888	1.265		1.013	1.055	U
		0.547					1.178	U
0.776	0.922	0.833					0.942	U
0.091	-1.173	1.167					0.080	uc
		1.002			-0.790	-2.246	-1.507	D
		0.739					1.002	U
							0.739	U
							0.990	U
-0.667							-0.667	D
							1.709	U
		0.445					0.445	U
-1.353	-2.141	-0.296		-1.713	-1.686	-2.429	-1.027	D
-1.115	-1.155	-1.129					-1.603	D
							-0.935	D

the downward gradient same to the latter, in spite of being a forest species. Therefore, the degree of differential responses seems parallel to the degree of differentiation of genetic characters, though the alternative interpretation, only behavioural responses becoming different between sibling relatives is not excluded.

Indubitably such gradient cannot fully be explained by the adult biology alone. The breeding site preference, for instance, either hypogaeic or phytophilous, must play a profound influence upon the adult distribution. Unfortunately, there is virtually no precise information about immature biology of drosophilid flies. This serious lack in *Drosophila* ecology must be fulfilled through further studies.

2. *Stratification of structure and daily fluctuation of drosophilid assemblage in undergrowth layer*: The vertical vegetation structure is considerably different between forest and grassland. In forest the space from the ground surface to the canopy is distinctly stratified with a resulting microclimatic differentiation. In grassland such the environmental stratification is poorer because of the simpler vegetation structure.

Using Dansreau's system (Dansreau 1951), the structure of undergrowth layer of trap stations is schematically presented in Fig. 3, though not including quantitative information. In forest two layers were observed. One was the lower layer of 20~40 cm h, mainly composed of *Pachysandra terminalis*, *Rhus ambigua*, *Galium trifloriforme*, *Cardamine leucantha*, *Chloranthus japonicus*, *Hydrangea petiolaris* and *Smilacina japonica*, and the other the higher layer of about 120 cm h, composed of dense bamboo-grass, with sparse admixture of low shrubs (*Cephalotaxus harringtonia nana*, *Phellodendron amurense* var. *sachalinense*). The bistratal structure was constant throughout the seasons, though the lower layer became relatively poor in October for withering. In grassland, young larches (150~200 cm h) were afforested at 2~3 m intervals. After snow thawing, there were only withered grasses on the ground between larches. Predominant plants (*Poa annua*, *Dactylis glomerata*, *Artemisia montana*, *Oenothera biennis*, *Erigeron annuus*) sprouted in mid May and formed dense vegetation of 80~120 cm h in early August. *Taraxacum officinale* and *Trifolium repens* were observed below this dense vegetation (at 20~30 cm h). This vegetation structure was kept constant till late autumn but became gradually poor in late October or early November by withering. These differences in vegetation structure are referred to in the subsequent discussions.

2.1. *Assemblage structure at four different heights in different seasons*: A. Forest (Fig. 4-A<sub>1-3</sub>): Total individual numbers were clearly different between two higher traps and two lower ones, that is, significantly higher at the former in June and August (A<sub>1,2</sub>), but without marked difference in October (A<sub>3</sub>). As shown in the former section, most forest species showed the constant upward gradient, except *quinaria* group and *D. testacea*.

The space below the canopy is suitable for various animals because of the

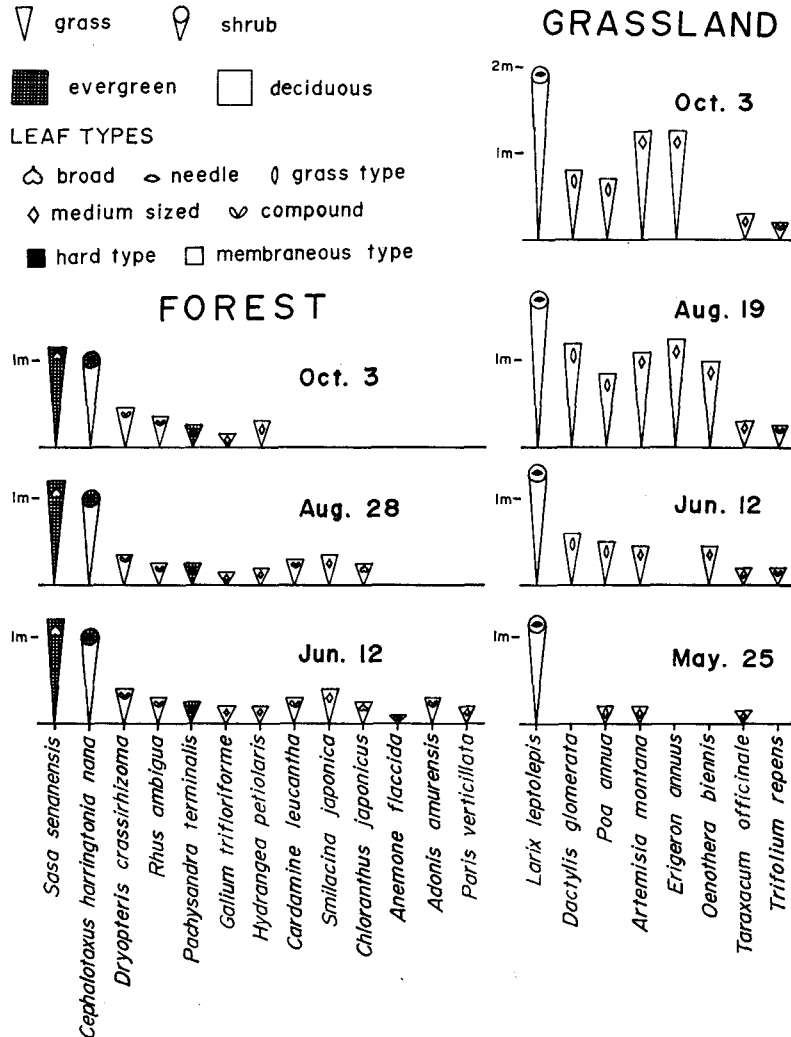


Fig. 3. Seasonal change of vegetation structure in forest and grassland.

protection from severe climatic conditions. Collected individual numbers were apparently lower at two lower traps set in dense bamboo vegetation. Therefore, the main flight space of drosophilid flies may lie between the upper surface of the undergrowth layer to the canopy. This conclusion is supported to some extent by the results by Greuter (1963) and Krizelj (1968).

Obviously assemblage components were mainly forest species in all seasons. The clear predominance of a few species and resulting simple assemblage structure

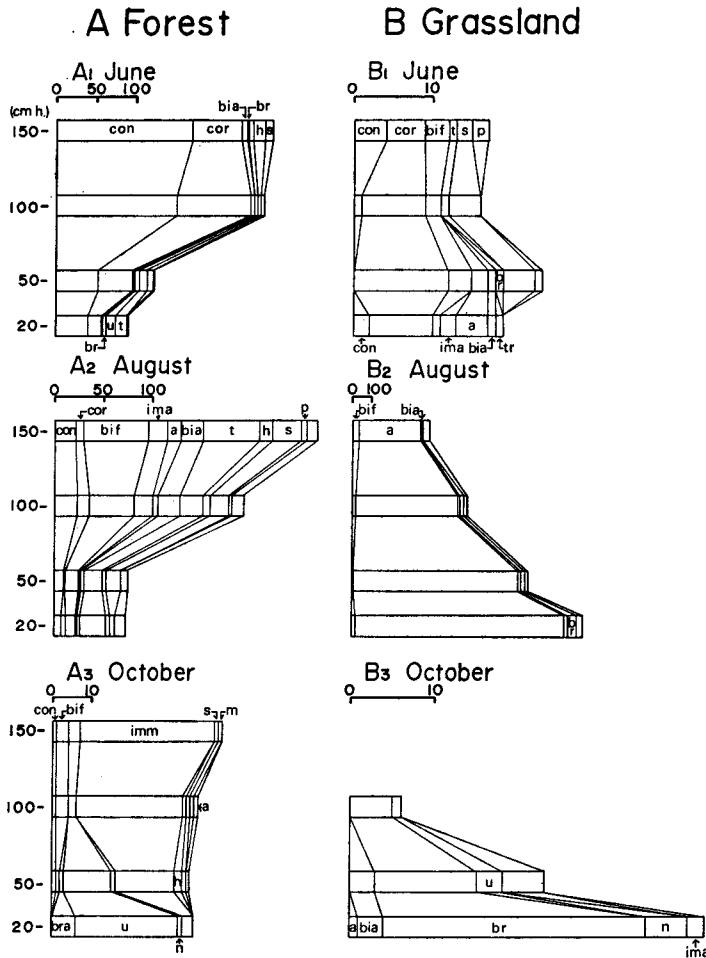


Fig. 4. Seasonal change of assemblage structure at different heights in forest and grassland. Main predominant species are symbolized as follows: con, *D. confusa*; cor, *D. coracina*; bif, *D. bifasciata*; ima, *D. imaii*; a, *D. auraria*; bia, *D. biauxuraria*; tr, *D. triauraria*; t, *D. testacea*; n, *D. nigromaculata*; br, *D. brachynephros*; u, *D. unispina*; h, *D. histrio*; imm, *D. immigrans*; s, *D. sordidula*; m, *D. moriwakii*; p, *D. pengi*.

were observed in June and October ( $A_{1,3}$ ), while the structure was more complex in August ( $A_2$ ). These differences in assemblage complexity seem to depend on the seasonal difference of population growth of each species. The presence of numerous species in summer is explained by the probable concentration of population peaks of various species due to favourable environmental conditions. In spring and autumn, environmental conditions are in general so severe that only

certain species adapted to such conditions could flourish.

B. Grassland (Fig. 4-B<sub>1-3</sub>): In June (B<sub>1</sub>) the assemblage was mainly composed of forest species defined previously (Toda 1973), showing a complex structure. There was no clearly predominant gradient in vertical distribution so that total individual numbers collected at four different heights were approximately equal. In August and October (B<sub>2,3</sub>), the assemblage was mainly composed of grassland species, showing a simpler structure. Main component species and total individual number showed the downward gradient.

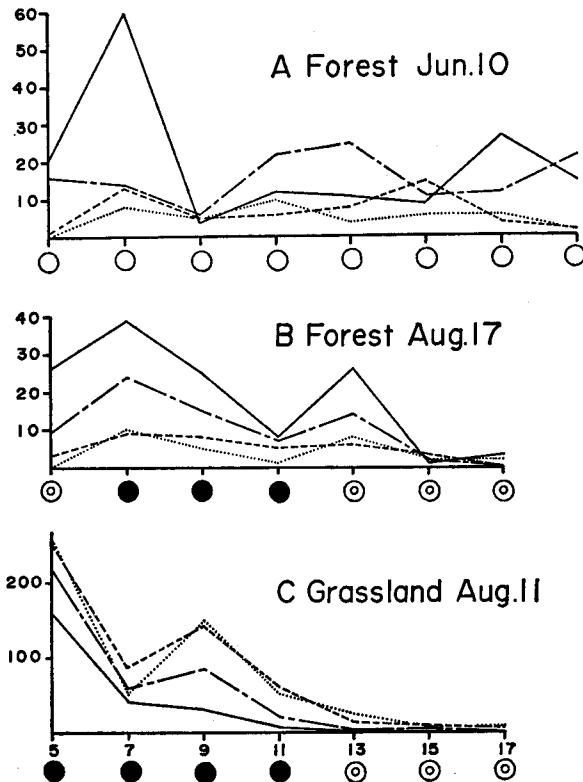


Fig. 5. Daily fluctuation of assemblage size at different heights in forest and grassland (solid: 150cm h. chain: 100 cm h. broken: 50 cm h. dotted: 20 cm h.).

The seasonal population growth of grassland species may be correlated with the development of the vegetation in grassland. The main components in June (B<sub>1</sub>) are forest species dispersed from neighbouring forests. Absence of predominant gradient in vertical distribution may be the outcome of occasional visits of forest species and undeveloped vegetation. In August (B<sub>2</sub>), the populations of grassland species reach the peak, in parallel with development of vegetation. The results obtained on the vertical distribution show apparently a clear limitation of grassland species to the thinner vegetation layer, because of severer climatic



and food conditions in the aerial space above the vegetation layer. When the vegetation was declining in October ( $B_3$ ), the gradient became very steep, with no specimen collected at 150 cm h, apparently indicating the reduced life zone of grassland drosophilids by plant withering.

2.2. *Daily fluctuations of drosophilid assemblages at different heights:* In forest (Fig. 5-A, B), two different daily patterns were observed between two higher

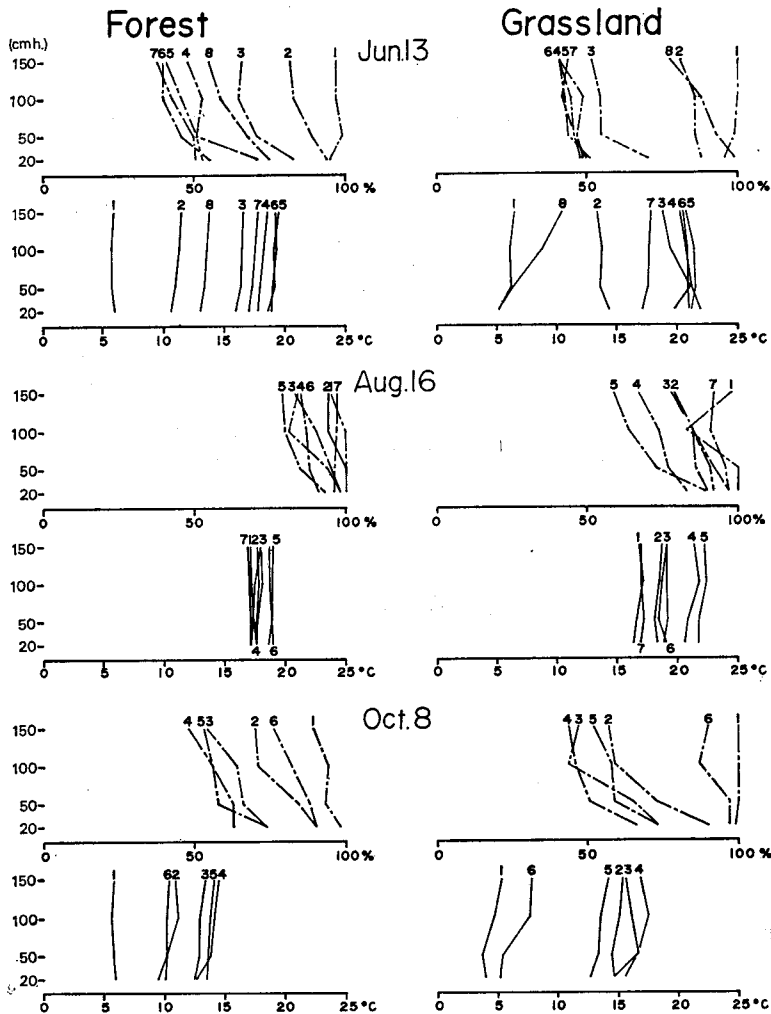


Fig. 6. Vertical change of air temperature (solid) and relative humidity (chain) from 20 cm h. to 150 cm h. in forest and grassland. The details on the observation time, general weather and wind class are as follow.

	Forest			Grassland		
	Time	General Weather	Wind Class	Time	General Weather	Wind Class
Jun. 13						
1	5:09	○	0	5:38	○	0
2	7:06	○	0	7:34	○	0
3	9:13	○	0	9:42	⊕	1
4	11:11	○	0	11:39	○	1
5	13:04	○	1	13:39	○	1
6	15:11	○	0	15:39	○	1
7	17:07	○	0	17:36	○	0
8	19:08	○	0	19:36	○	0
Aug. 16						
1	5:02	⊕	0	5:28	⊙	0
2	7:41	⊙	0	8:07	⊙	1
3	9:05	⊙	1	9:31	⊙	0
4	11:06	⊙	1	11:32	⊙	0
5	13:01	⊙	1	13:26	⊙	1
6	15:07	⊕	1	15:33	⊙	1
7	17:07	●	0	17:32	⊙	1
Oct. 8						
1	7:07	○	1	7:33	○	1
2	9:12	⊕	1	9:38	⊕	1
3	11:13	⊕	1	11:38	⊕	1
4	13:13	⊕	2	13:39	⊕	1
5	15:12	⊕	2	15:39	○	1
6	17:08	○	1	17:34	○	1

traps and two lower ones, that is, a sharp periodicity with several distinct peaks in the former and a lower activity with no clear midday decrease in the latter. In grassland (Fig. 5-C), such remarkable difference was not observed among fluctuation patterns at different heights, though the assemblage at lower traps showed higher activities and longer active periods than those at higher ones.

The differences observed in forest seem to depend upon the plant stratification in the undergrowth layer described at the beginning of this section. Two lower traps were set in the dense bamboo-grass layer and higher ones on or above the upper surface of the undergrowth layer. The vertical patterns, not so different in grassland, may be due to a simpler structure of the vegetation layer.

From readings of temperature and relative humidity from 20 cm h to 150 cm h, only inconspicuous temperature differences were observed between higher and lower positions. The gradient with daily changes fluctuated in different weathers and seasons. On the other hand, relative humidity constantly showed a downward gradient in both vegetations. This gradient became steeper in midday than in morning or evening (Fig. 6).

Two different daily patterns between higher and lower traps in forest appear-

ed to be parallel to such humidity conditions. The assemblage size at higher traps fluctuates accompanied with wide daily change of humidity, with abrupt midday decrease at lower humidity. On the other hand, the obscure periodicity at lower traps may be due to more stable and higher humidity near the ground. This does not contradict the hypothesis of behavioural adaptation to relative humidity mentioned in the former section.

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### Summary

The studies on daily activity and vertical microdistribution of drosophilid flies were made in Misumai Arboretum of Hokkaido University in Sapporo City in 1971. Flies were collected at four different heights in undergrowth layer of forest and grassland for four days each in June, August and October, using fermented banana baits.

Most predominant species showed bimodal crepuscular activities, except *D. coracina* which had a specific unimodal activity with a midday peak. The mechanism of behavioural adaptation to daytime aridity and the interspecific significance on feeding periodicity were discussed with respect to such specific daily activity patterns.

Seasonal fluctuations of daily activity patterns were observed in *D. brachynephros*, *D. unispina* and probably *D. immigrans*, and the importance of temperature in autumn as a factor controlling daily activity patterns was pointed out.

Most species showed relatively high plasticity in their daily activities as in humid tropic Brazilian species, contrasting to the relatively fixed periodicity of *D. pseudoobscura* preferring arid habitat. It was assumed that the behavioural adaptation rather than physiological resistance to desiccation is connected with such plasticity.

In vertical microdistribution, most forest species except *D. unispina* and *D. testacea* showed the upward gradient, against grassland species showing the downward gradient. From the comparison of *D. auraria* and *D. brachynephros*, it was pointed out that, though vertical distribution pattern is generally paralleled with the vertical gradient of environmental factors, this does not always mean the similarity in relative importance of various factors for each species.

From the consideration of assemblage structure at four different heights of

forest and grassland in different seasons, it was concluded that in forest, the main flight range of drosophilid flies is confined to the space between the upper surface of the undergrowth layer to the canopy, while the grassland species develop their populations, accompanied with vegetation growth, and are limited in the thinner vegetation layer.

In forest, the daily fluctuation patterns of assemblages at lower traps showed a periodicity less distinct than those at higher ones, probably caused by the constantly higher relative humidity near the ground.

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