A Preliminary Study on Microdistribution and Dispersal in Drosophilid Natural Populations

By

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(With 4 Text-figures and 2 Tables)

Since Timoféeff-Ressovsky and Timoféeff-Ressovsky (1940a, b, c) pointed out the necessity of quantitative information on natural drosophilid populations for genetic studies, several papers have been published on the dispersal of drosophilid populations. In this field American investigators (Dobzhansky and Wright 1943, 1947, Burla *et al.* 1950, Richardson 1968, 1969) dealt with the precise analysis on a single species from the stand point of population genetics, while European ones (Burla and Greuter 1959a, b, Greuter 1963) were concerned about the interspecific relation for habitat preference between two closely allied species, *Drosophila obscura* and *D. subobscura*. The theoretical works (Wallace 1966a, Wright 1968), based on the study by Dobzhansky and Wright (1943), have advanced with regard to some aspects of pouplation genetics, e.g., the rate of elimination of lethal genes by homozygosis in *D. melanogaster* (Wallace 1966b), etc. On the other hand, even basic information on dispersal behavior in natural conditions is virtually absent for many species.

In previous papers (Toda 1973a, c) I reported the vegetational preference on some species inhabiting Hokkaido, but not microdistribution. It was noticed that some forest species frequented traps placed in open clear cut area. This suggests their wide-roaming nature visiting from surrounding forests, but their actual flight range has been unknown. The present study was conducted to obtain simultaneously the basic information on microdistributions and dispersal of various species inhabiting the same area. Furthermore, the procedure is characterized by multipoints releasing method, by which the nature of dispersal in natural conditions must more accurately be represented than by one-point releasing usually adopted by other investigators.

Before going further, I wish to express my sincere thanks to Dr. Shôichi F. Sakagami for his pertinent guidance in the course of the present study, and to Prof. Mayumi Yamada for his reading through the manuscript. Cordial thanks are also due to Dr. Tatsuichi Tsujii, Botanical Garden, Hokkaido University, for his allowance of the free use of

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Misumai Arboretum for the present study, and Prof. Eizi Momma, who allowed me the use of culture stocks of several species for practice of marking technique, and Mr. Masato Kimura for his kind help in collecting materials and giving valuable suggestions in preparing the present paper.

Method

The study was carried out from July 27 to August 25, 1973, at Misumai Arboretum of Hokkaido University (cf. Toda 1973a) in the suburb of Sapporo City. The surveyed field was chosen in the area where grassland was encroaching upon natural forest. This grassland was cleared by bulldozers in 1971, thereafter it has recovered for two years as a vegetation well developed as before operation. The grassland is surrounded in three directions by natural broad-leaved forests with well developed undergrowth of bamboo-grass.

In total 29 traps were placed in a cross-shaped fashion, separated 20 m for each other, the center situated at the middle part of grassland. Three arms of the cross are penetrated into the surrounding forest (Fig. 1). The traps used are polyethylene pails (2 litre in capacity) baited with fermented banana.

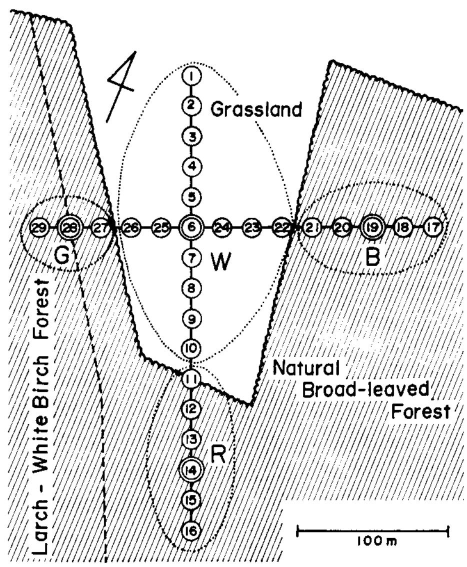

Fig. 1. The survey field showing a cross-shaped arrangment of traps, with indication of the use of different colors for marking. The releasing points are doubly circled.

Wild flies inhabiting the survey field were used for marking. Collections of flies for marking were carried out as a rule in three periods a day; morning (5:00～8:00), midday (11:00～14:00) and evening (16:00～18:00), though evening collections were omitted on some days. In each collection period all 29 traps in the cross-shaped field were visited two or three times. All flies of Dorosophilidae collected in each period were narcotized by ethylether and marked by a gentle push of lacquer sprayer enough to put several small color

Table 1. Sequence of marking (M) and release (R) trials. (T: Total, W~G: Colors).

Date	Marking Hour	Numbers of marked flies and release hour				T
		W	R	B	G	
Jul. 27	M 5:00~:55, 7:20~ 8:10	11	42	24	10	87
	M 11:00~:55, 12:00~:50, 13:00~:50	1	74	60	37	172
	M 16:00~:55, 17:00~:50	5	8	8	3	24
	T	**17**	**124**	**92**	**50**	**283**
	R	(18:40)	(18:55)	(18:48)	(18:38)	
Aug. 3	M 5:05~:58, 6:02~:50, 7:00~:42	14	43	51	10	118
	R	(11:05)	(11:17)	(11:35)	(11:51)	
	M 10:58~11:55, 12:58~13:55	15	54	83	8	160
	R	(17:46)	(17:50)	(17:58)	(17:44)	
	T	**29**	**97**	**134**	**18**	**278**
Aug. 5	M 5:07~6:02, 6:07~:54, 7:00~:40	10	9	10	5	34
	R	(13:06)	(13:17)	(13:35)	(13:48)	
	M 11:00~:49, 13:02~:49	1	33	26	7	67
	R	(16:07)	(16:16)	(16:30)	(16:44)	
	M 16:03~:47, 17:00~:43	5	3	5	6	19
	R	(18:19)	(18:26)	(18:21)	(18:16)	
	T	**16**	**45**	**41**	**18**	**120**
Aug. 10	M 5:13~6:10, 6:14~7:01, 7:05~:48	13	52	54	12	131
	R	(11:19)	(11:31)	(11:49)	(12:08)	
	M 11:10~12:06, 13:01~:50	7	72	70	26	175
	R	(16:14)	(16:26)	(16:40)	(16:52)	
	M 16:08~:53, 16:58~17:37	7	30	17	10	64
	R	(18:29)	(18:37)	(18:32)	(18:41)	
	T	**27**	**154**	**141**	**48**	**370**
Aug. 12	M 5:08~:57, 6:01~:35, 6:59~7:27	12	15	13	5	45
	R	(11:03)	(11:12)	(11:25)	(11:35)	
	M 10:59~11:37, 13:00~:35	0	24	11	9	44
	R	(-)	(16:15)	(16:25)	(16:35)	
	M 16:04~:37, 16:55~17:26	0	4	9	6	19
	R	(-)	(18:12)	(18:17)	(18:08)	
	T	**12**	**43**	**33**	**20**	**108**
Aug. 17	M 4:59~5:57, 6:00~:42, 6:59~7:27	26	57	130	20	233
	R	(11:05)	(11:15)	(11:32)	(11:46)	
	M 11:01~:48, 13:09~:50	2	27	32	6	67
	R	(17:15)	(17:23)	(17:18)	(17:13)	
	T	**28**	**84**	**162**	**26**	**300**
Aug. 24	M 5:58~6:49, 7:00~:40	6	30	52	11	99
	R	(11:08)	(11:19)	(11:33)	(11:45)	
	M 11:04~:44, 13:00~:36	3	18	20	2	43
	R	(16:06)	(16:17)	(16:31)	(16:39)	
	M 16:02~:41, 16:59~17:36	13	16	12	1	42
	R	(18:27)	(18:35)	(18:30)	(18:39)	
	T	**22**	**64**	**84**	**14**	**184**
TT		**151**	**611**	**687**	**194**	**1,643**

dots on the body and wings of each fly. From the laboratory test, it was suggested that this marking technique has probably no effect on flies at least in culture bottles. Four colors were used to discriminate the flies captured in different parts within the cross-shaped field; white (W) in grassland (Trap Nos. 1~10, 22~26), red (R) at Trap Nos. 11~16, blue (B) at Trap Nos. 17~21 and green (G) at Trap Nos. 27~29, the latter three in forest. Only total individual number of marked flies was recorded for each color, because it is impossible to identify the species by naked eyes in field. Thirty minutes to three hours later, the marked flies awaked in glass tube were released on the ground at the following releasing points; W: No. 6, R: No. 14, B: No. 19 and G: No. 28. However, on July 27 whole flies marked in morning, midday and evening were released at the same time in evening. In this way marking and release were carried out for seven days (Table 1). Recaptures were made seven times at two hours interval from 5:00 to 17:00 on the next day of each marking-day, except on August 18, when collections could be done only four times because of the heavy rain.

Both marked and unmarked flies collected at each trap were removed from the survey field by putting them into a small glass vial containing 70% alcohol. Bringing these samples to the laboratory, the specimens were identified and examined as to the presence or not of marks under a binocular microscope.

Results and Discussions

In total 1,643 individuals (W: 151, R: 611, B: 687, and G: 194) were marked throughout the survey period. It must be noted that the real numbers of marked flies are unknown but probably smaller than these numbers, since the marking procedure adopted in the present study inevitably permits the same individual to be marked more than two times. Among them 339 individuals (W: 33, R: 114, B: 136, G: 50, WR: 1, RB: 3, and RG: 2, the last three ones bicolored) were recaptured, together with 1,770 unmarked flies consisting of 25 species belonging to three genera (Table 2). As for unmarked flies, the heterogeneity of population densities between grassland and forest, or among different marking areas (shown by mark colors) in forest was analysed by chi-square test. Further, the distribution pattern within each vegetation or each color area in forest was analysed by Morisita's $I\delta$ method (Morisita 1959).

$$I\delta = q\frac{\Sigma x_i(x_i-1)}{N(N-1)}$$

where q=the number of traps, N=the total number of unmarked individuals, and x_i=the number of unmarked individuals captured at Trap No. i. $I\delta$ takes the value of unity, if the individuals are distributed at random over the area. When the individuals are distributed uniformly over the area, $I\delta$ will take the value smaller than unity, and if the distribution is contagious, $I\delta$ will be larger than unity. The significance of the departure from randomness of the distribution can be tested by the comparison of F_0 with the value of $F^{q-1}_{\infty}(a)$, the former given by the following formulae.

When $I\delta \geq 1$, $F_0=\dfrac{I\delta(N-1)+q-N}{q-1}$

Table 2. Drosophilid flies collected throughout the survey period. Marked individuals are separately shown for each color (symbols explained in text), together with unmarked individuals. * Previously reported as *Drosophila rufifrons* Okada 1956.

Species	Unmarked	Marked						
		W	R	B	G	WR	RB	RG
Drosophila testacea	512	-	7	8	3	-	-	-
D. coracina	485	10	73	63	34	-	3	2
D. biauraria	185	2	11	12	-	-	-	-
D. bifasciata	173	2	8	18	3	1	-	-
D. sordidula	115	2	9	16	2	-	-	-
D. confusa	62	-	-	-	-	-	-	-
D. imaii	37	-	-	1	-	-	-	-
Amiota variegata	37	1	-	-	-	-	-	-
Drosophila pengi	28	-	1	7	1	-	-	-
D. immigrans	27	3	5	11	6	-	-	-
D. brachynephros	25	-	-	-	-	-	-	-
D. suzukii	15	-	-	-	-	-	-	-
D. histrio	14	-	-	-	-	-	-	-
D. nigromaculata	11	8	-	-	-	-	-	-
**D. throckmortoni*	10	-	-	-	-	-	-	-
D. unispina	8	-	-	-	-	-	-	-
D. melanogaster	6	3	-	-	-	-	-	-
D. auraria	6	2	-	-	1	-	-	-
D. lacertosa	5	-	-	-	-	-	-	-
D. busckii	3	-	-	-	-	-	-	-
D. lutea	2	-	-	-	-	-	-	-
D. triauraria	1	-	-	-	-	-	-	-
D. ezoana	1	-	-	-	-	-	-	-
Leucophenga stenomaculipennis	1	-	-	-	-	-	-	-
Amiota sp.	1	-	-	-	-	-	-	-
TOTAL	1,770	33	114	136	50	1	3	2

When $I\delta<1$, $F_0=\dfrac{(1/I\delta)(N-1)+q-N}{q-1}$

In the following part the nature of microdistribution and dispersal is referred to for each predominant species and some others, separately.

a) *D. coracina*: In total 485 unmarked individuals were captured throughout the whole period, whose distribution is shown with hatched histogram in Fig. 2–A. The densities between grassland and forest are significantly different at the 1 per cent level. The typical silvicolous nature of this species is obvious from Fig. 2–A. As for the distribution in forest, the densities are significantly different in R–G, and B–G, while not different in R–B.

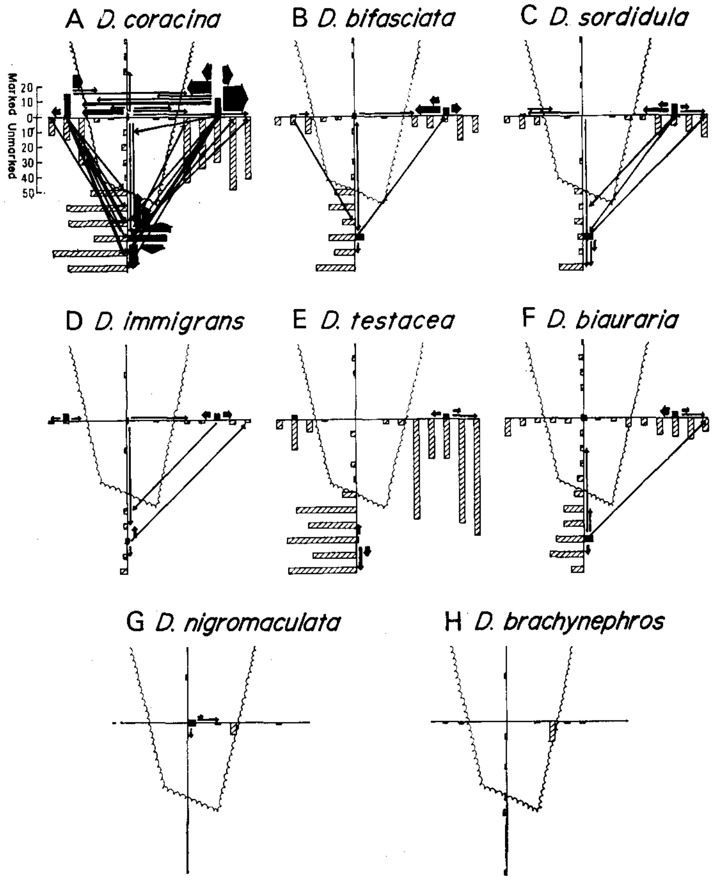

Fig. 2. Microdistribution of unmarked individuals and dispersal of marked ones in eight species (A~H). Unmarked individuals, marked ones recaptured at the releasing points and marked ones having dispersed are shown respectively with hatched histogram, black histogram and black arrows. The two histograms and the width of the arrows are same scaled, as shown at top-lefthand of A.

	Grassland-Forest	B-R	R-G	B-G	B-R-G
Chi-square Value	447.898*	1.006	17.327*	23.308*	23.650*

*P<0.01

The departure of G from R and B is mainly due to the small number at Trap Nos. 28 and 29, the latter trap located within larch - white birch mixed forest and the former at the border between larch - white birch forest and natural forest, whereas both R and B in natural broad-leaved forest. This suggests the influence of forest types upon the distribution. The $I\delta$ value of the distribution over the natural forest is 1.026, without significant departure from randomness. In other words, the individuals are distributed approximately at random over the area, since the value of F_0 (2.038) is smaller than the value of F (2.405) at the 5 per cent level.

	$I\delta$	F_0	$F_{\infty}^{q-1}(0.05)$	$n_1=q-1$	Distribution Pattern
Natural Forest	1.026	2.038	2.405	11	Random

The amount of marked individuals recaptured throughout the whole period was the largest among all species. The dispersal done by these recaptured individuals is shown with black arrows, except the individuals recaptured at the releasing points shown with black bars (Fig. 2-A). As for the individuals released in forest, those recaptured at traps near the releasing points in forest were significantly more than those having migrated to grassland beyond the forest edge, while *vice versa* in the individuals released in grassland. This outcome, as well as the microdistribution described above, indicates clearly attachment to forest. The marking experiment indicates that even some individuals occasionally visiting neighboring grassland may not stay for a long time but return to forest soon. It is interesting to inspect the individuals recaptured in the areas different from those where they were released. Such distant dispersal was relatively frequent in G–R, and R–B not separated by other habitats, without particular trends in directions. Furthermore, the recapture of five bicolored individuals, three RB and two RG, indicates the relatively frequent dispersal among G–R–B. Natural forest and larch - white birch forest were recognzied above as somewhat different habitats for this species, but the mutual dispersal between them occurs to some extent, since one migrant No. 14→No. 29 and three No. 28→No. 29 were recaptured. The mutual dispersal between B and G separated by grassland about 120 m wide were observed thrice, two B→G and one G→B. Although the possibility of dispersal via R within continuous forest is not excluded, the direct dispersal across the grassland is likely, judging from some distant transhabitat dispersal such as No. 19→No. 26 and No. 19→No. 7. The procedure adopted in the present study does not permit to estimate the dispersal rate, but the migrants recaptured on July 28, all released in evening of the preceding day, may indicate the direct dispersal distance per day. Distant migrants among them were two, No. 28→No. 11 and No. 28→No. 15, or about 120 m and about 200 m in distance, respectively.

The results given above are based upon the summarized data throughout the whole period, but it should not be ignored that the activity of drosophilid flies is strongly affected by climatic conditions and has a diurnal rhythm. In Fig. 3-A the daily activity patterns of unmarked individuals in forest and grassland are separately shown for fine (August 4), cloudy (August 11) and rainy (August 18) days. The high midday activity on fine days is the regular nature of this species in Hokkaido (Shima 1960, Kaneko 1968, Toda 1973b), and was confirmed in the

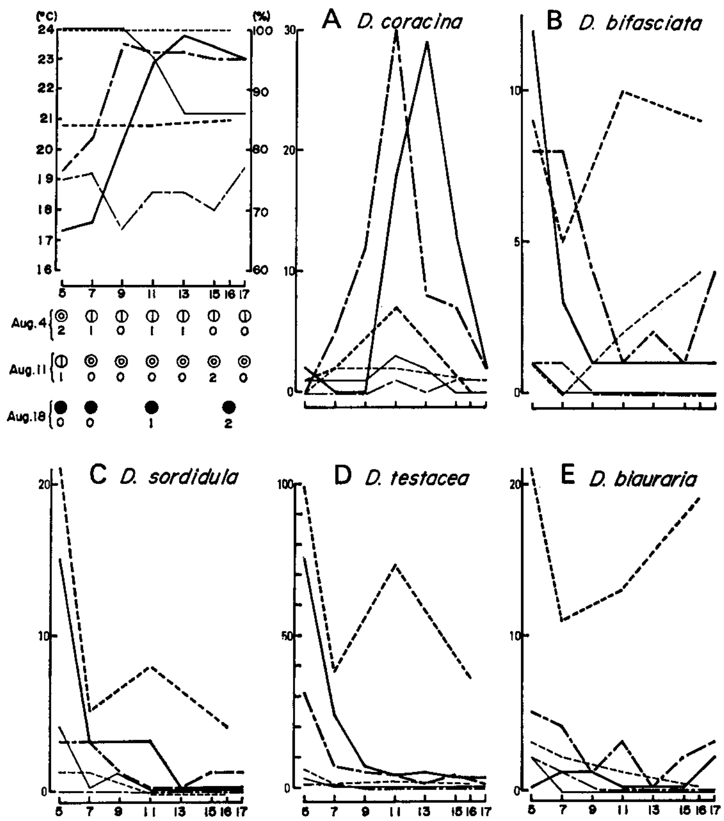

Fig. 3. Daily activity patterns of unmarked individuals in forest (thick lines) and grassland (thin lines) in different climatic conditions: fine (Aug. 4), solid; cloudy(Aug. 11), chain; rainy (Aug. 18), broken. The data on general weather, air temperature (thick), relative humidity (thin), and wind class observed at Trap No. 14 during the corresponding periods are shown at top-lefthand.

present study, too. The most important outcome from the figure is the discrepancy of patterns between forest and grassland on the same day. If it is assumed that the individuals flying to grassland are those activated extremely in forest during the active period, the higher the activity in forest is, the more flies would be captured in grassland, resulting in a correspondence between daily patterns in both vegetations. Consequently, the discrepancy described above suggests that flying to grassland may be rather accidental or physiologically abnormal, though without crucial evidence. In Fig. 4 the microdistribution pattern of unmarked individuals and dispersal features by marked ones in different climatic conditions are shown for morning, midday and evening separately. Although dispersals

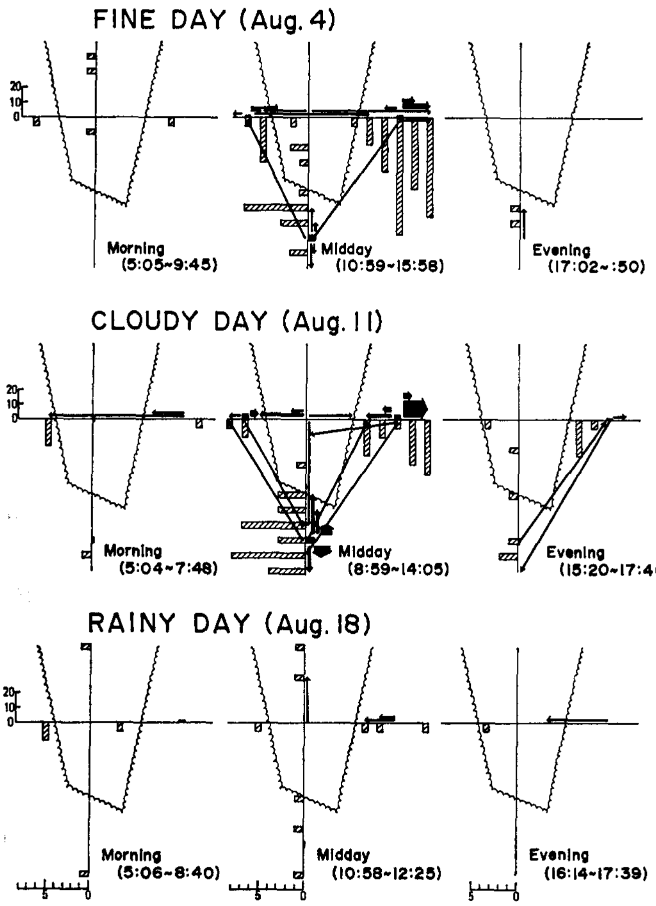

Fig. 4. Daily changes of microdistribution and dispersal of *D. coracina* in different climatic conditions.

illustrated in each figure include not only those made just during the period but also some ones made before, the dispersal features seem to show that most dispersals also take place in midday under favorable climatic conditions.

To summarize, *D. coracina* is a typical forest species and is distributed at random over the natural broad-leaved forest surveyed in the present study. The dispersal is considerably frequent within the natural forest, mainly occurring in midday on fine days. Moreover, some migrants beyond grassland about 100 m wide were observed. From these facts, it is guessed that this species builds up an almost uniformly mixed population within the surveyed area, though the term "uniformly mixed population" is used here purely in ecological sense, not implying the genetical usage. The habitat of this species seems to spread over a continuous forest on mountain slopes in Hokkaido, but with a heterogeneity in density within it, which is caused by various forest forms due to different component tree species.

b) *D. bifasciata*: The silvicolous nature reported in previous papers (Toda 1973a, c) is clearly shown in microdistribution of unmarked individuals (Fig. 2–B). The chi-square values indicate that the density in R is significantly higher than in B and G.

	Grassland-Forest	B-R	R-G	B-G	B-R-G
Chi-spuare Value	135.475*	8.584*	11.408*	1.071	15.994*

Although $I\delta$ value among all trap stations within the forest shows a contagious distribution, $I\delta$ among three different color areas in forest (evaluated from x_i= average individual number per trap in each area instead of individual number at particular trap, and q=the number of areas=3 instead of the number of traps) shows the randomness, as well as the distribution within each area in forest.

	$I\delta$	F_0	$F^{q-1}_{\infty}(0.05)$	$n_1=q-1$	Distribution Pattern
Forest (among traps)	1.168	3.055	2.206	13	Contagious
Forest (among areas)	1.055	1.844	19.496	2	Random
B	1.111	2.249	5.628	4	Random
R	1.060	2.104	4.365	5	Random
G	1.071	1.710	19.496	2	Random

The manner of dispersal is, though not so obvious, similar to that of *D. coracina*. The daily activity patterns in grassland approximately correspond to those in forest (Fig. 3–B), implying that individuals flying out to grassland, though being rare, may be those activated in morning on fine days or throughout the day in rainy condition.

In conclusion, this species, one of the typical forest species in Hokkaido, is distributed almost continuously within the surveyed forest but with a heterogeneity in density. The causes of this heterogeneity within a forest probably homogeneous in environmental conditions remain unsolved, but Dobzhansky and his colleagues (Dobzhansky and Wright 1943, 1947, Dobzhansky and Epling 1944) described in *D. pseudoobscura*, belonging to the *obscura* group as *D. bifasciata*, the heterogeneous distribution with highly dense clumps in the neighborhood of old or diseased oak and pine trees. In spite of such heterogneiety, the population within the surveyed forest is guessed as well mixed.

c) *D. sordidula*: This is also a typical forest species (Fig. 2–C). The evaluated $I\delta$ value shows the contagious microdistribution within the forest.

	Grassland-Forest	B-R	R-G	B-G	B-R-G
Chi-square Value	85.329*	4.185	0.039	3.211	5.516

	$I\delta$	F_0	$F^{q-1}_{\infty}(0.05)$	$n_1=q-1$	Distribution Pattern
Forest	1.213	2.704	2.206	13	Contagious

The result of recapture is very similar to that in *D. bifasciata* (Fig. 2–C), both probably holding the dispersal features similar to those in *D. coracina* described above. The daily activity patterns in grassland correspond to those in forest as well as in *D. bifasciata*. In conclusion, this species is considerably similar to *D. bifasciata* both in microdistribution and dispersal, though the former may build up more tight clumps within the population than the latter.

d) *D. immigrans*: Against only 27 unmarked individuals caught throughout the whole period, the number of recaptured marked individuals is relatively high (Table 2). The manner of dispersal is as like as those in three forest species described above. The previous studies on the seasonal activity in Hokkaido on this common domestic species accord in the regular autumn burst in forest near human habitations (Wakahama 1957, Kaneko 1960, Kaneko and Tokumitsu 1963, Toda 1973a). It is postulated that this species increases its population from spring to summer in and near human habitations, then invades into neighboring forest, forming there a homogeneous and well mixed population from late summer to autumn. This annual cycle may be repeated every year, since this species seems impossible to hibernate in wild environments at least in Hokkaido, although crucial evidence must be acquired by future studies.

e) *D. testacea*: The number of unmarked individuals caught throughout the whole period is the top ranked, followed by *D. coracina*. This forest species was distributed in significantly different densities among different color areas in forest, contagiously within each area (Fig. 2–E).

	Grassland-Forest	B-R	R-G	B-G	B-R-G
Chi-square Value	476.424*	26.427*	35.665*	86.551*	93.482*

	$I\delta$	F_0	$F_{\infty}^{q-1}(0.05)$	$n_1=q-1$	Distribution Pattern
Forest (among traps)	1.363	14.766	2.206	13	Contagious
Forest (among areas)	1.257	13.310	19.496	2	Random
B	1.162	11.652	5.628	4	Contagious
R	1.116	5.524	4.365	5	Contagious
G	1.246	5.059	19.496	2	Random

Comparing with the large amount of unmarked individuals, only few marked individuals were recaptured near and at the releasing points in forest, which suggests an extremely low recapture rate since it is supposed that the amount of marked individuals was approximately the same as the former. The causes of this low recapture rate are unknown. Some possible factors are heavy damage by marking, escape to forest canopy, emigration out of the surveyed area, etc. Among them the first mentioned factor is relatively plausible, because this species is one of the smallest ones in Drosophilidae, though it may not always accord with the delicacy or physiological weakness. As for the escape or emigration representing a high migratory capacity, I can say nothing on both in the present study. On the other hand, if the obtained result implies the sedentary nature of this species, it is inferred that the population in the surveyed forest is divided into subpopulations. This hypothesis is supported by the contagious distribution of unmarked individuals. Finally, the individuals rarely captured in grassland is regarded as those flying out from forest during active period, since the daily activity patterns in grassland somewhat correspond to those in forest (Fig. 3-D).

f) *D. biauraria*: Although this species obviously prefers forest to grassland (Fig. 2-F), the continuous distribution in grassland suggests the ability to survive there, too.

	Grassland-Forest	B-R	R-G	B-G	B-R-G
Chi-square Value	82.410*	2.225	7.964	2.619	8.520

Furthermore, the departure of daily activity patterns between both vegetations; approximately bimodal with morning and evening peaks in forest, while unimodal with only morning peak in grassland (Fig. 3-E), was observed. In a previous paper (Toda 1973b) dealing with vertical microdistribution in undergrowth layers, it was noticed that the gradient of this species was reversed between grassland and forest, while that shown by migrants of *D. bifasciata* did not change in grassland. These facts indicate indirectly that a considerable part of the individuals collected in grassland are not migrants from forest but residents. The $I\delta$ value in each vegetation indicates the random distribution,

	$I\delta$	F_0	$F_{\infty}^{q-1}(0.05)$	$n_1=q-1$	Distribution Pattern
Forest	1.137	2.581	2.206	13	Random
Grassland	0.963	1.090	2.131	14	Random

but Fig. 2-F shows a marked but gradual decrease from forest to grassland, showing no abrupt change at forest edge. The dispersal seems relatively frequent within the forest and probably takes place in some degree between both vegetations. The comparison of this species with its close relative, *D. auraria*, being recognized as a typical grassland species (Toda 1973a, b, c), is the most fascinating problem. But, the latter species was too scarce for such consideration in the present survey.

g) *D. nigromaculata* and *D. brachynephros*: Only these two rare species showed the distinct preference for grassland, attached contagiously at one trap station (No. 22) where the vegetation was the densest within the grassland (Figs. 2-G, H). *D. nigromaculata* is collected by sweeping bushes at well developed grassland of coltsfoots and others, or along streams and paths through forest (Toda unpubl.). The habitat preference for grassland in *D. brachynephros* was reported in previous papers (Toda 1973a, b). The dispersal of marked individuals of *D. nigromaculata* released in grassland was limited within a small area near the releasing point (Fig. 2-G).

Remarks

As mentioned in introduction, the present study was conducted to obtain basic information for microdistribution and dispersal in natural drosophilid populations. The obtained data are too insufficient for mathematical analyses of density of wild populations from recapture rates, mean dispersal rates and distances in a particular period, etc. Further, even the basic information obtained may or may not include some deviations from the natural conditions of populations, due to the method adopted in the present study. In the following part several problems with regard to such possible deviations are considered.

It is first pointed out whether the microdistribution of individuals attracted to baits represents accurately the natural conditions, or more precisely, whether the attractiveness of baits is different between different environments, e.g., grassland and forest. This problem can be partly solved by using other collecting methods. For instance, as described for *D. nigromaculata*, the information obtained by sweeping supports the vegetational preference of this species obtained by bait traps in the present study. In future, in order to understand the actual microdistribution of drosophilid natural populations, much information on life mode of each species, especially feeding and breeding habits in natural conditions, must be acquired, which are seriously neglected at the present.

In several previous studies on the dispersal of drosophilid flies (Dobzhansky and Wright 1943, 1947, Burla *et al.* 1950, Burla and Greuter 1959a, Greuter 1963), as well as in the present study, the experimental fields were designed as cross-shaped, L-shaped or linear series of bait traps. It is possible that dispersal of released individuals is affected by these designs, as well as microdistribution of wild individuals described above. Especially, such effects may not be neglected when exposing traps throughout the survey period as in the present study. This problem can be partly avoided by exposing traps only at the time of recapture.

Although fruit traps have been used in all previous studies on dispersal in drosophilid populations, the defects on microdistribution and dispersal by using bait traps have been relatively ignored. Concerning the general validity of using bait traps, it is worthy to mention the comment by Dyson-Hudson (1956): "Collections of *D. subobscura* made by suction traps (Tayler and Kalmus 1954) 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". The activity studied by suction traps may represent that of flight and dispersal. It is, therefore, implied that feeding activity likely corresponds to flight and dispersal one. This hypothesis is supported by another fact described previously (Toda 1973c) that many flies of *D. moriwakii* and others are resting still in shady favorable conditions, for instance, the shade of plant roots overhang on cliffs, in midday when they are in an inactive phase. Consequently, the general utility of bait traps is reasonable for studying dispersal in drosophilid populations.

Concerning the problems involved in the release and recapture procedure for studying dispersal behavior in natural drosophilid populations, Parsons and McKenzie (1972) pointed out that the marked individuals are released from a crowded situation, which would tend to yield an overestimate of dispersal. From a laboratory experiment, Sakai *et al.* (1958) divided migrations in *D. melanogaster* into two kinds; namely, "random migration", which occurs as a result of random movement of individual flies, and "mass migration" resulted by high population pressure. The latter density dependent migration must play a role in the crowded situation at release. As the most suitable technique to avoide this defect, the neutron activation techniques to label drosophilid flies in natural populations were invented by Richardson *et al.* (1969).

This technique consists of admixture of rare earth and other elements in bait and neutron activation analyses. In contrast to the release of lab-cultured individuals (Timoféeff-Ressovsky and Timoféeff-Ressovsky 1940b, c, Dobzhansky and Wright 1943, 1947, Burla *et al.* 1950, Burla and Greuter 1959a, b, Greuter 1963), or of those marked in the field (the present study), this labeling techique is easily used with the populations normally residing in the study area, without giving disturbance by capture and marking. In spite of much usefulness this technique has not yet been used, except for the studies by Richardson (1968, 1969). He added a 0.03 M 2% sucrose solution of dysprosium acetate as labeling element to the fruit bait of the central trap. The flies collected over the study area were brought into the laboratory and analysed whether dysprosium was present or not in each fly.

Although the results reported in the present paper involve some defects, the obtained basic information is useful for further population ecological studies, and will be incorporated in precise genetic analysis of drosophilid natural populations.

Summary

1) A preliminary study on microdistribution and dispersal in drosophilid natural populations was carried out from July 27 to August 25, 1973, at Misumai Arboretum of Hokkaido University in the suburb of Sapporo City. The survey field was designed in a cross-shaped fashion, extending over grassland and forest.

2) Wild flies inhabiting the survey field were used for marking. They were marked with four different colors to distinguish the flies captured in four different parts within the field, and released separately at a definite point within respective part. In total 1,643 individuals were marked, among which 339 individuals were recaptured together with 1,770 unmarked flies.

3) The results on microdistribution of unmarked individuals and dispersal of marked ones were separately shown for six forest species (*D. coracina, D. bifasciata, D. sordidula, D. immigrans, D. testacea* and *D. biauraria*) and two grassland species (*D. nigromaculata* and *D. brachynephros*). Based upon the results obtained, the nature of the population inhabiting the survey field was briefly discussed for each species. Three forest species, *D. coracina, D. bifasciata* and *D. sordidula*, were

relatively similar in the general nature of populations, though slightly different in microdistribution for each other. It was guessed that they build up well mixed populations within the surveyed forest and spread over a continuous forest on mountain slopes in Hokkaido with a heterogeneity in desity. As for *D. immigrans*, a common domestic species, it was postulated that this species increases its population from spring to summer in and near human habitations, then invades into neighboring forest, forming there a homogeneous and well mixed population from late summer to autumn. In *D. testacea* the obtained data showed a relatively sedentary nature and the division into subpopulations within the surveyed forest. However, these results were uncertain because of the low recapture rate. It was mentioned that a fraction of the *D. biauraria* population within the survey area inhabited the grassland, too. The two grassland species were sedentary, though available data were poor. Thus, each species differed characteristically in microdistribution or dispersal.

4) Some considerations were given on the possible deviations of the results from natural conditions due to the method adopted.

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