Kontyû, **47**(4): 443–455. December 25, 1979

Habitat Segregation of the Drosophilid Flies in the Vicinity of Streams

Katsura BEPPU*

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

Synopsis Habitat preferences of the drosophilid flies were investigated in the vicinity of streams. Four species of the *robusta* group (*D. okadai, D. neokadai, D. lacertosa* and *D. moriwakii*) and two species of the *virilis* group (*D. ezoana* and *D.* sp. 4) were supposed as streamside dwellers. In the upper or middle part of the stream *D. ezoana* preferred open stony streamsides, and *D. okadai* and *D. neokadai* preferred stony streamsides. Though *D. lacertosa* was abundant at various streamsides, they preferred more canopied streamside. *D. moriwakii* was abundant not only at the streamside but also in the streamside forest. In the lower reaches *D.* sp. 4 preferred willow groves in the vicinity of the stream. Some flies of *D. lacertosa* were also seen in mentioned groves with *D.* sp. 4. From these facts, it is assumed that habitat of each streamside dweller is species specific.

Up to the present, a great numbers of studies have been made on the habitat preference of drosophilid species, and streamside was recognized as one of drosophilid habitat. However, no comprehensive ecological studies have hitherto been carried out in the vicinity of the streamside.

On the other hand, it is common that the closely related species in phylogeny have similar life modes in the basic requirement of resources. According to the previous reports (TAKADA, 1958 a, b; KANEKO and SHIMA, 1962; KANEKO and TAKADA, 1966; KANEKO, MOMMA and SHIMA, 1967; KANEKO, MOMMA and TOKUMITSU, 1968; KANEKO, TOKUMITSU and SHIMA, 1968; KANEKO and TOKUMITSU, 1969; TODA, 1973), streamside dwellers of the drosophilid flies in Hokkaido were belonging to the *virilis* or the *robusta* species group, which are derived from the *virilis-repleta* radiation (THROCKMORTON, 1975). Therefore, it is attempted to bring together such fragmentary information concerning streamside species in Hokkaido, and more detailed surveys on their microdistributions were carried out in the central part of Hokkaido. In this paper microdistributions of the wild species of the *robusta* group and the *virilis* group were treated, and some discussion on the adaptive radiation of the old world *virilis-repleta* radiation in Hokkaido are done.

Streamside environments change continuously from the headwaters to the estuary. Here, two types of environments of such various parts of a stream were

* Present address: Hokkaido Experimental Forest of Kyûshû University, Ashorobuto, Ashoro, Hokkaido 089–37, Japan.

selected for this investigation. One is the upper or middle part of the stream where current runs through forests, and the other is the lower reaches where bushes or groves are seen along the streamside.

Before going further, the author wishes to express his sincere thanks to Prof. Eizi MOMMA for his kind advice. Cordial thanks are also due to Dr. Masahito T. KIMURA and Mr. Masanori J. TODA for their useful suggestion. This paper is based on a part of the doctor thesis presented to Hokkaido University.

Areas Studied and Methods

Six localities (Nopporo, Moiwa, Soranuma, Jozankei, Ban-nosawa and Nanporo) were selected for this investigation in or near Sapporo City, the central part of Hokkaido. Abbreviations of each locality are as follows; Nopporo (NF), Moiwa (MF), Soranuma (SR), Jozankei (JZ), Ban-nosawa (BS) and Nanporo (NA), and location of them is shown in Fig. 1. General environmental conditions at NF, MF and JZ were shown in BEPPU (1976), at SR were in KIMURA *et al.* (1978), and at BS and NA were in the below.

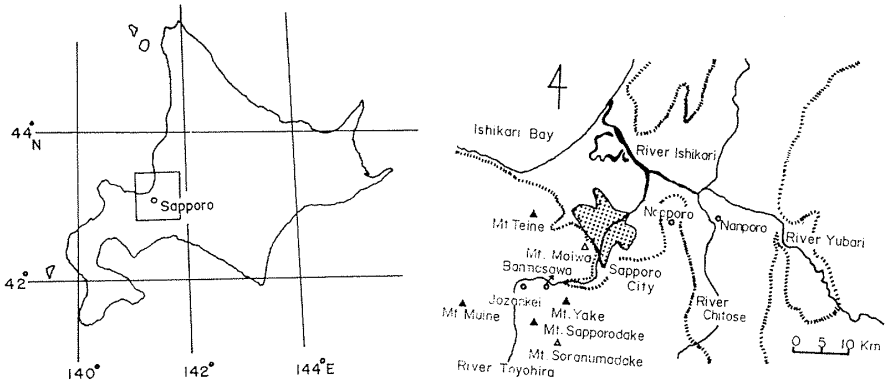

Fig. 1. Location of the area studied.

In the present study either milk can trap (MC) collections or retainer trap (RT) collections were performed. Both types of the traps were baited with fermenting banana.

There are two types of collections in the MC collections, and each collection is codified as follows;

H_1, H_2: Each collection is done by one hour intervals (H_1) from 5: 00 to 10: 00 (7: 00 to 12: 00 in Oct.), or two hour intervals (H_2) from 5: 00 to 17: 00 (7: 00 to 17: 00 in Oct.).

D_1, D_2: Mentioned H_1 or H_2 collection is done for a day (D_1), or for successive two days (D_2).

By means of the RT, either continuous collections or one week collections once in each month were performed throughout the season. Codes of such collections were as follows;

CO: Continuous collections throughout the season. Stored flies were removed at weekly intervals, together with bait renewal.

W_1: Baited RT were set for a week once in a month.

1. The upper or middle part of a stream

Microdistributions of streamside drosophilids were surveyed from the following three aspects;

Survey 1: The degree of restriction to streamside environments.

Survey 2: Preferences for streamside microtopographical or vegetational differences.

Survey 3: Vertical microdistribution.

According to TODA and KIMURA (1978), in addition to the mentioned abbreviations, methods

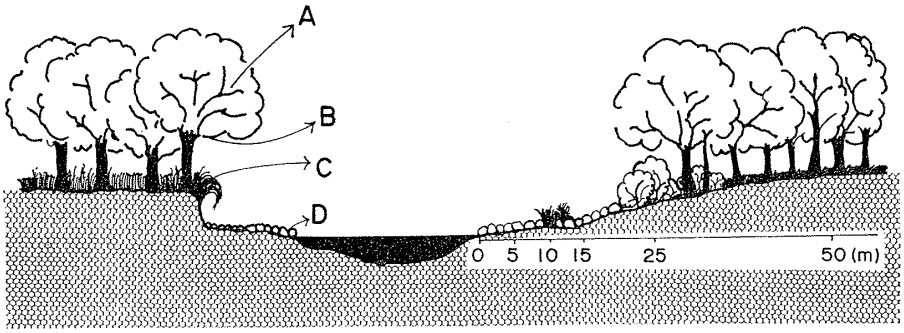

Fig. 2. Schema of microenvironments around trap spots of the Survey 1 and 3.

of each survey are codified as follows;

Survey 1: Tf-JZ, MF, NF-'74, and Tf-SR-'75 (Area studied was set at the foot of Mt. Soranuma. Altitude is about 350 m). By means of six MC, H_2D_2 were carried out from May to October at NF, but from July to October at other three localities. Traps were set at intervals of 0, 5, 10, 15, 25 and 50 m from the stream edge at each locality (Fig. 2). The width of the stream in each locality is as follows; MF=0.5 m, NF=1.0 m, SR=2.0 m and JZ=10.0 m (*cf.* BEPPU 1976).

Survey 2: Tf-JZ-'76. By means of eight MC, H_1D_1 was carried out from May to October once in each month. Microenvironments of each trap spot are shown in Fig. 3. Roman numerals show the spots at main stream streamsides and small letters of the roman alphabet show the ones at branch streamsides (*cf.* BEPPU 1978).

Survey 3: Tf-BS, SR-'76. Considering the faunal differences at main and branch streamsides, two types of the trap stations were selected at both localities; one was a canopied streamside (I) and the other was a open streamside (II). Four RT were set at each trap station as shown in Fig. 2 (A: in the canopy of the streamside tree, B: under part of the canopy, C: in front of the cliff shelter

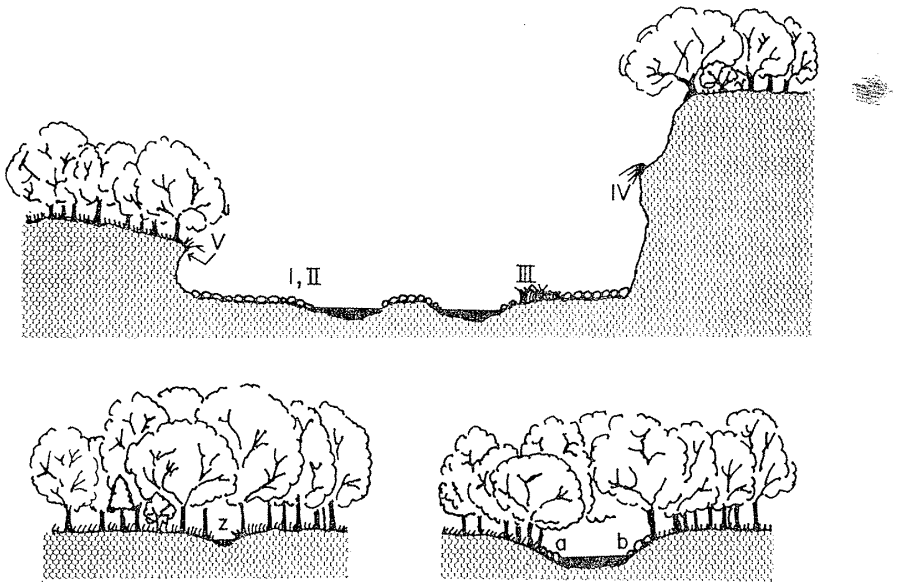

Fig. 3. Schemata of microenvironments around trap spots of the Survey 2.

or in the shrub layer of the forest floor, and D: streamsides), and CO were carried out from May to the beginning of November.

Ban-nosawa is located about 17 km southwest of the center of Sapporo City. Trap spots were set along the upper part of the branch stream of the Toyohira River. This branch is about 2 m in width and the upper part is running through the deciduous broad-leaved forest, which consists of *Quercus crispula etc.*, but the lower part is running through the grassland. Human habitations are seen near the confluence of this branch and the Toyohira River.

Traps in SR were set at the streamside of the main and the branch stream of the Yunosawa. Width of the branch and the main is about 0.3 m and 3 m respectively (This branch is different from the one used in the Survey 1).

2. The lower reaches of a stream

The streamside environments of the lower reaches are fundamentally different from those of the mentioned upper or middle part; *e.g.* the former having only a moderate growth of willow groves in the vicinity of a stream against the latter surrounded by well developed broad-leaved deciduous forests. The lower reaches are inhabited by a peculiar member of streamside dwellers, *D.* sp. 4 together with *D. lacertosa*.

The area studied (NA) was set at the lower reaches of the Chitose River (Fig. 1). The river is about 30–50 m in width at this area and dry riverbed was about same width. The streamside environments are roughly divided into two types; 1) willow groves are seen along the riverside, and 2) grassland or bush was seen from the edge of the river. Most part of the dry riverbed was covered by short-tall grassland. Codes of this area is as follows; Tf-NA-'78. By the use of eight RT, W_1 was carried out from May to October. Traps were set in the various environments of the riverside, and such spots were shown in Fig. 8 schematically. Four traps shown by the roman alphabet (A, B, C and D) were set in the willow grove of the streamside, and other four shown by roman numerals (I, II, III, and IV) were set on the dry riverbed.

Results and Discussion

In the upper or middle part of a stream all streamside species except for *D.* sp. 4 were abundant, but in the lower reaches only *D.* sp. 4 was abundant.

1. The upper or middle part of a stream

1.1 Individual numbers of collected specimens at each spot in the Survey 1 were shown in Table 1. The composition of drosophilid species of the *robusta* and the *virilis* group species is different in each locality; *D. lacertosa* and *D. moriwakii* were abundant in all localities, *D. okadai* and *D. neokadai* at JZ and SR, but *D. ezoana* only at JZ.

The percentage distribution patterns of each species are shown in Fig. 4. From the figure two types of habitat preferences are distinguished: one is strongly restricted to the streamside environments (*D. ezoana, D. okadai, D. neokadai* and *D. lacertosa*), and the other has broader preference not only to the streamside but also to the surrounding forests (*D. moriwakii, D. sordidula,* and *D. pseudosordidula*). According to TODA (1973, 1977), habitat of *D. sordidula* is situated in the shrub layer on the forest floor. Therefore, dependence to the streamside environments of *D. sordidula* is weaker than that of other *robusta* group species, though they were

Table 1. Collected number of flies at each trap spot in the Survey 1.

Locality	Distance from water's edge of the stream					
	0	5	10	15	25	50 (m)
D. lacertosa						
Jozankei	21	25	3	3	2	—
Moiwa	36	32	7	1	1	2
Soranuma	47	3	3	3	—	—
Nopporo	443	162	117	80	18	8
D. okadai						
Jozankei	48	101	10	1	2	1
Moiwa	2	—	1	—	—	—
Soranuma	115	9	6	1	2	—
Nopporo	4	—	1	—	—	—
D. neokadai						
Jozankei	34	18	1	3	—	—
Moiwa	No specimens were collected					
Soranuma	135	6	2	1	—	—
Nopporo	16	5	1	—	—	—
D. moriwakii						
Jozankei	3	2	28	10	19	8
Moiwa	86	111	114	37	26	30
Soranuma	373	277	212	388	165	97
Nopporo	54	26	82	51	39	57
D. sordidula						
Jozankei	1	—	—	1	1	—
Moiwa	1	1	—	—	—	—
Soranuma	26	9	13	29	19	12
Nopporo	1	—	1	—	—	—
D. pseudosordidula						
Jozankei	3	—	—	2	1	—
Moiwa	2	1	—	—	—	—
Soranuma	4	1	11	7	12	2
Nopporo	10	2	8	—	2	3
D. ezoana						
Jozankei	158	61	2	—	—	—
Moiwa	No specimens were collected					
Soranuma	2	—	—	—	—	—
Nopporo	No specimens were collected					

collected fairly abundantly in the vicinity of streams. At the present stage of knowledge, too much cannot infer on the habitat of *D. pseudosordidula,* but habitat preference of this species seems to be similar to that of *D. sordidula* (BEPPU unpubl.).

From these facts, two adaptive radiations are assumed in the *robusta* group: one is to the streamside (*D. okadai, D. neokadai* and *D. lacertosa*) and the other is to the forest floor (*D. sordidula* and *D. pseudosordidula*), and *D. moriwakii* shows intermediate type of the mentioned two.

1.2. As shown in the Survey 1, compositions of streamside species varied

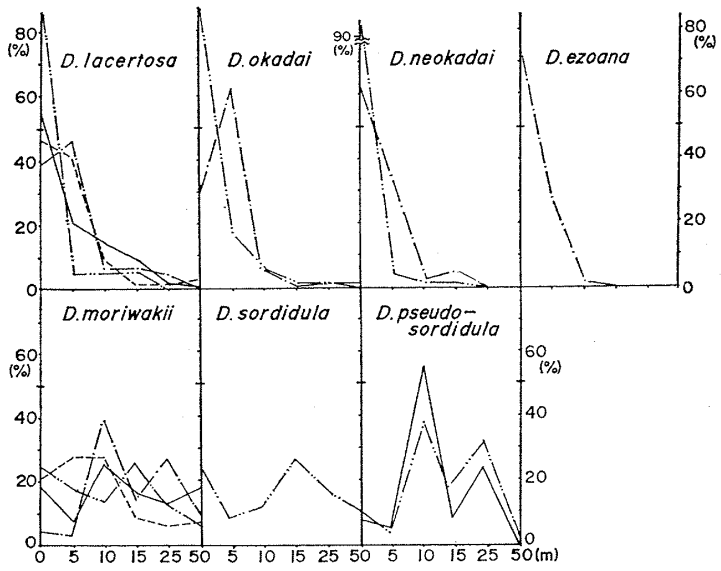

Fig. 4. Horizontal microdistribution patterns of the streamside dwellers and two relatives (Solid: Nopporo, Broken: Moiwa, Chain: Jozankei, and Two dots chain: Soranuma).

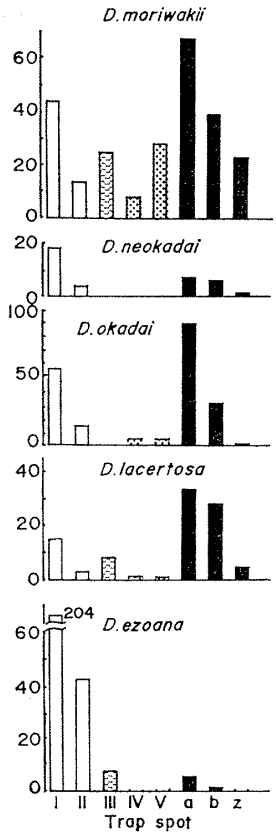

Fig. 5. Microdistributions of the streamside dwellers at various environments in the vicinity of streams (White: Streamsides of the main stream, Hexagon: Bush on the dry riverbed, Dots: Cliff Shelter, and Black: Streamsides of the branch streams).

from a locality to a locality. Such variations seem to be attributed in part to the microtopographical or vegetational differences of the collecting spots. It is, therefore, supposed that there are some differences in preferences for such variables among streamside species, even among the four species strongly restricted to waterside environments. In the Survey 2 these preferences were surveyed.

Microdistributions of the five species, which show the dependence to streamside, were shown in Fig. 5. Abundance of *D. ezoana* is characteristic of the main stream streamside where there are stones, small rocks and/or fallen trees, but no sandy soil or pebbles. This means that *D. ezoana* prefers open stony streamside such as a main or uncanopied stream. A similar trend shown by *D. ezoana* was reported by HERTING (1955) for *D. littoralis,* which also belongs to the *virilis* group. These facts suggest that mentioned open stony waterside may be the main habitat of the wild *virilis* group species.

D. lacertosa is abundant both at main and branch streamside, and abundance of this species at every locality where the Survey 1 was carried out is suggestive that this species has broader preferences for the various streamside than other streamside dwellers. However, this species is more abundant at the branch streamside (Fig. 5).

Table 2. Number of collected flies of streamside dwellers and two relatives at each trap spot in the Survey 3 (I: Canopied streamsides, and II: Open streamsides).

Soranuma	I-A	II-A	I-B	II-B	I-C	II-C	I-D	II-D	Total(I)	Total(II)
D. ezoana	—	—	—	—	—	2	—	27	—	29
D. okadai	—	—	—	—	—	1	—	5	—	6
D. neokadai	—	—	—	—	—	—	—	4	—	4
D. lacertosa	—	1	—	2	—	2	1	18	1	23
D. moriwakii	97	94	149	444	179	116	13	159	438	813
D. sordidula	16	41	16	93	49	185	6	33	87	352
D. pseudosordidula	—	—	4	3	5	5	—	1	9	9
Total	113	136	169	542	233	311	20	247	535	1,236
Ban-nosawa										
D. ezoana	—	1	3	1	4	4	5	43	12	49
D. okadai	—	—	—	—	—	—	—	4	—	4
D. neokadai	—	—	—	—	—	—	1	1	1	1
D. lacertosa	1	2	7	8	10	9	11	11	29	30
D. moriwakii	1	8	8	6	8	8	1	—	18	22
D. sordidula	102	297	375	237	761	1,270	79	170	1,317	1,974
D. pseudosordidula	1	1	—	1	4	5	—	1	5	8
Total	105	309	393	253	787	1,296	97	230	1,382	2,088

Therefore, this species may prefer the canopied streamside (*cf.* BEPPU 1978).

Preferences of *D. okadai* and *D. neokadai* were not so restricted as *D. ezoana,* but not so wide as *D. lacertosa.* They were collected in some abundance both at main and branch streamside, but less so at the streamside of the very narrow stream like spot 'z' regardless of some abundance of *D. lacertosa.* This trend is supported by the data of the Survey 1 at MF and NF. Consequently, restriction of *D. okadai* and *D. neokadai* to the streamside would be connected with stony waterside environments. In behavioral observation in the field, several flies of these two species were found in the cracks among damp stones at the streamside or on the dry riverbed. This suggests that the existence of the crack among such stones or small rocks seems to be necessary as resting sites for their life in native environments. Flies of *D. lacertosa* showed such behavior, but they flew in under the leaves of the streamside grasses or fern which hung over the stream. By this fact it is supposed that they would be able to live at the streamside of the mentioned narrow stream.

D. moriwakii did not show any trend in this survey. This would be due to the weaker water dependence as shown in the Survey 1.

1.3. By the mentioned surveys habitats of streamside dwellers were revealed horizontally. The other aspect of habitat separation is the vertical microdistribution in the space above stream surface. The vertical microdistributions were surveyed in the Survey 3.

Numbers of collected specimens of the *robusta* group and *D. ezoana* are shown in Table 2. Further, percentage distribution patterns of four species are shown in

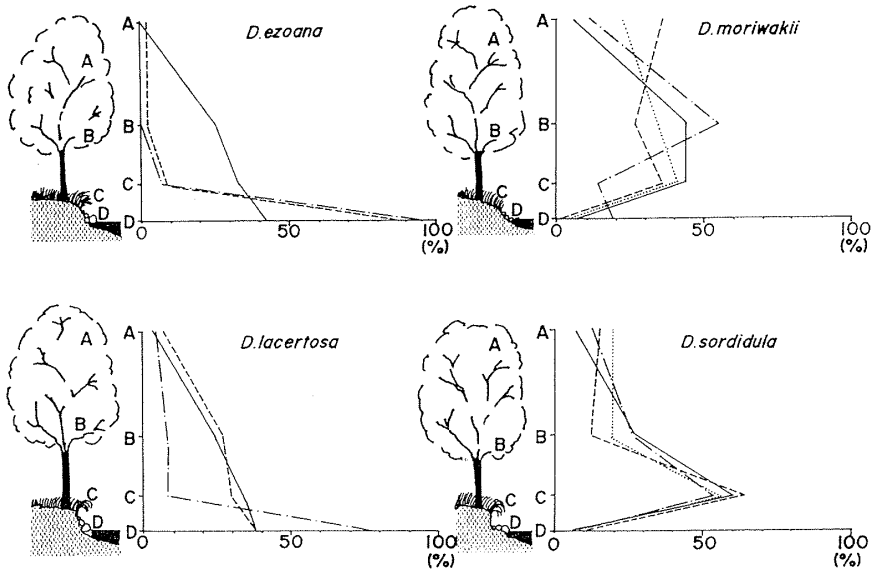

Fig. 6. Vertical microdistribution patterns of three streamside species and *D. sordidula* (Solid: BS-I, Broken: BS-II, Dots: SR-I, and Chain: SR-II).

Fig. 6. According to these data, *D. ezoana, D. okadai, D. neokadai* and *D. lacertosa* were strongly restricted to water surface, though more or less variations in the degree of the restriction are seen. *D. moriwakii* which is abundant at spots B and C overlaps largely with *D. sordidula* and *D. pseudosordidula* which are abundant at spot C.

However, collected numbers of flies of *D. okadai* and *D. neokadai* are very small so that analyses for their preferences are not sufficient. Therefore, behavioral observation for these species were carried out in the early morning at SR in 1976. Results obtained from this observation are shown in Fig. 7. Both circles (black and white) show the point where fly of each species stopped for a while and feeding or resting was seen. However, black circles show the point of the two species (*D. okadai* and *D. neokadai*), because though morphological differences between *D. okadai* and *D. neokadai* exist, especially in genitalia, those are so slight that it is impossible to distinguish these two species in observations of the naked eyes. In spite of such defects, this figure shows that active space of *D. okadai* and *D. neokadai* is more restricted to the streamside than that of *D. moriwakii*. This fact supports the mentioned trend obtained from the trap collections.

To sum up the mentioned facts, *D. ezoana* is distributed vertically in a limited space just above water surface at open streamside, and *D. okadai* and *D. neokadai* are also restricted to the limited space above stream surface as well as *D. ezoana*. *D. lacertosa* is the most abundant at D, but a number of specimens were collected at higher traps. Therefore, this species also prefers the space above stream surface, but its range of the vertical distribution extends more upwards than those of *D. ezoana, D. okadai* and *D. neokadai*. This suggests that *D. lacertosa* has a wider pre-

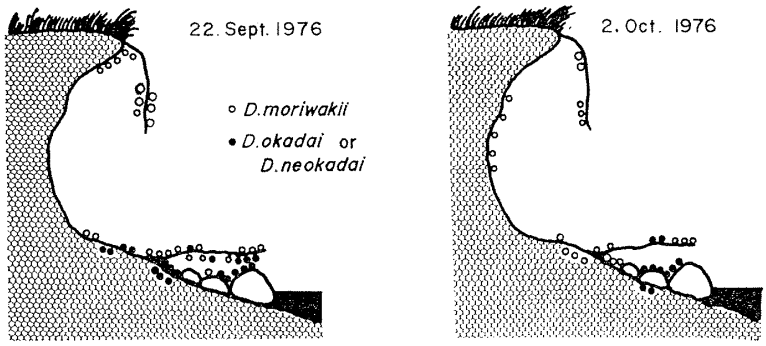

Fig. 7. Feeding or resting spots of three streamside dwellers.

ference than *D. ezoana, D. okadai* and *D. neokadai* not only horizontally but also vertically at open and canopied streamsides.

Compared with the mentioned four species, *D. moriwakii* is distributed abundantly from the undergrowth layer to the subarboreal layer in the streamside forests, and besides this species rested in the cliff shelter in daytime. Thus existence of such shelter is important for their distribution. Therefore, though *D. moriwakii* is regarded to be a streamside dweller, habitat preference of this species is not so specialized as those of the mentioned four.

In conclusion, the results of the vertical survey agree closely with the features found in the horizontal microdistribution.

2. The lower reaches of a stream

The streamside fauna of the lower reaches is conspicuously characterized by *D.* sp. 4, together with the sporadical distribution of *D. lacertosa.* As shown in Fig. 8, microdistributions of *D.* sp. 4 and *D. lacertosa* are restricted to the vicinity of the streamside, particularly to the willow grove along the stream. BLIGHT and ROMANO (1953) reported that *D. americana* which belongs to the *virilis* group was collected in a streamside willow grove. CARSON (1971) described in more detail that *D. americana* was reluctant to leave the grove of sandbar willow where this species bred. From these reports, it is supposed that restriction of *D.* sp. 4 and *D. lacertosa* to the streamside willow groves seems to be due to not only high humidity but also the existence of breeding materials. Further, places shaded by willow grove, as well as cracks of stones or under parts of fallen trees in the upper or middle parts of a stream, may serve as resting sites in daytime for this species.

In consequence, it is assumed that the streamside willow groves provide the indispensable conditions for the life of *D.* sp. 4 and *D. lacertosa.*

Concluding Remarks

As for the streamside dwellers of the drosophilid fly in Hokkaido, the exact

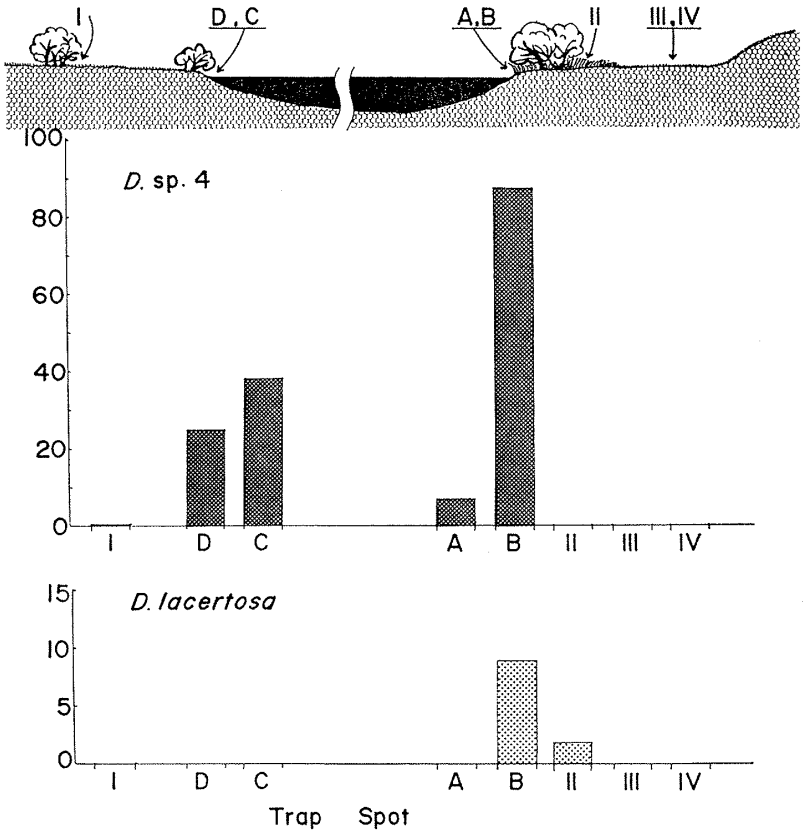

Fig. 8. Microdistributions of two streamside dwellers at various environments in the lower reaches of the stream.

features of their habitat preferences have remained obscure, though in the previous papers one can find several brief notes (*cf.* papers cited in the preface).

The present study revealed that there are two types of basic trends in habitat preferences of streamside dwellers: one is strongly restricted to the waterside and the other is widely distributed not only at the waterside but also in the streamside forests. Moreover, microdistribution patterns of individual species vary to some extent for each other according to differences of riparian environments. This suggests that species specific microdistribution pattern reflects their preferences to the kinds of resting sites, food resources and breeding sites *etc.*, and their tolerances to physical factors such as temperature, humidity and so on.

On the basis of the mentioned habitat preferences, it would be allowed to schematize the habitat of each streamside species and two forest dwellers of the *robusta* group as shown in Figs. 9 and 10.

In the upper or middle part of a stream (Fig. 9), streamside environments are shared by the four species, *D. lacertosa, D. okadai, D. neokadai* and *D. ezoana.* In these species *D. ezoana* prefers more open stony watersides such as the edge of the main stream, ponds or lakes. However, open wide sandy streamside lacks all

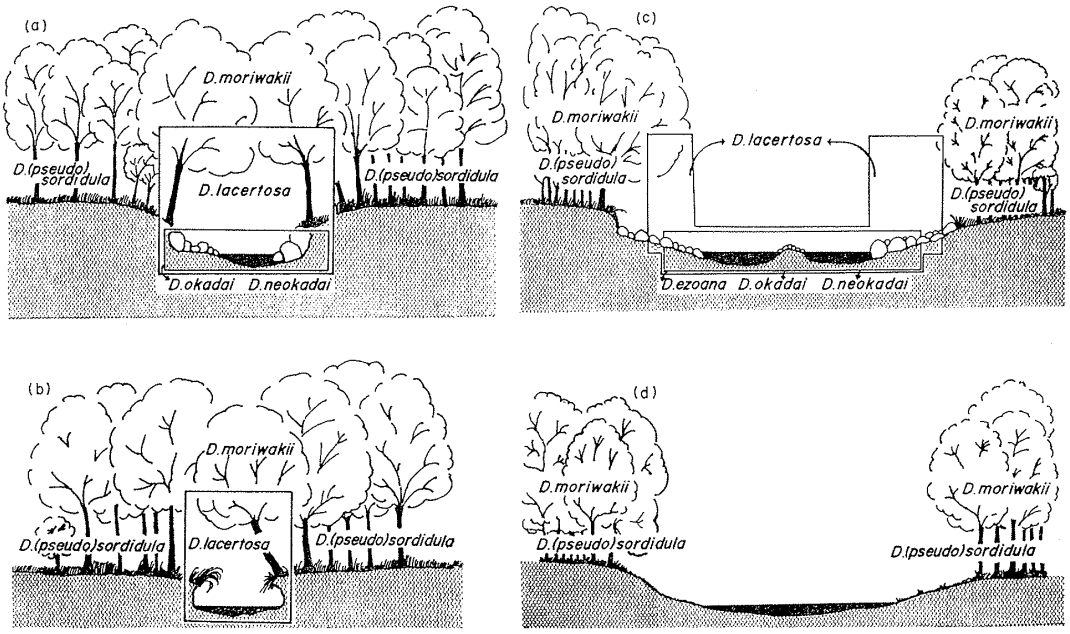

Fig. 9. Schemata of habitats of streamside dwellers and two relatives in the upper or middle part of the stream (a: Canopied stony streamsides, b: Canopied narrow streamsides, c: Open stony streamsides, and d: Open sandy streamsides).

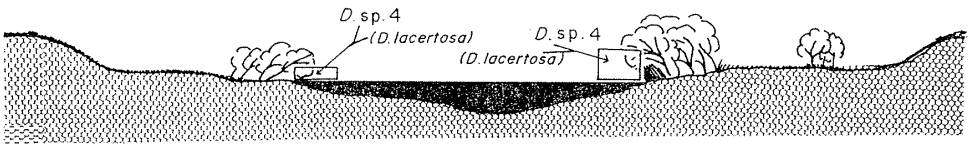

Fig. 10. Schema of habitats of two streamside dwellers in the lower reaches of a stream.

of the streamside species (Fig. 9 d). These would be due to the lacks of the resting site in daytime, breeding materials and so on. *D. okadai* and *D. neokadai* prefer the stony streamside irrespective of open or not, and active space of them is also restricted to water surface as well as *D. ezoana*. Habitat preference of *D. lacertosa* is wider than those of the mentioned three species both in horizontal and vertical space, though the trend that this species is abundant at the canopied streamside was seen.

D. moriwakii does not show so conspicuous restriction to the streamside as the mentioned four species, but their microdistribution is also restricted to the woodland streamside, particularly to the cliff shelter. Therefore, degree of the restriction to the streamside of *D. moriwakii* is intermediate between the mentioned four and the two species described in the below.

Remaining *robusta* group members in Hokkaido, *D. sordidula* and *D. pseudo-sordidula*, distributed in the shrub layer on the forest floor, but many flies were

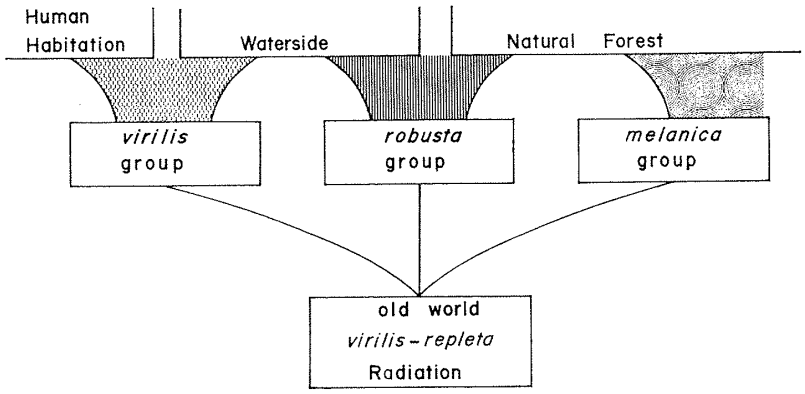

Fig. 11. Schema of the adaptive radiation of the old-world *virilis-repleta* radiation in Hokkaido.

collected in the vicinity of streams. Judging from microdistribution patterns of them, habitat of these two species overlaps more or less with that of *D. moriwakii*. This is suggestive that interspecific competition between these forest dwellers and *D. moriwakii* may exist for some resources.

In the lower reaches, *D.* sp. 4 and *D. lacertosa* are suitable members of the streamside dwellers. Microdistribution pattern shows that these two species prefer the streamside willow groves.

On the other hand, from a phylogenetical point of view it is revealed that streamside dwellers in Hokkaido consisted of the members of the two groups (*robusta* and *virilis*) which belong to the old world *virilis-repleta* radiation. According to THROCKMORTON (1975), the *melanica* group also belongs to this radiation, and these three groups (*robusta, virilis,* and *melanica*) show similar ecological features.

However, as mentioned above, two direction of the adaptive radiation are seen in the *robusta* group in Hokkaido: one is to the waterside and the other is to the forest floor. In the *virilis* group, *D. virilis* is known as a famous domestic species (*cf.* DOBZHANSKY 1965), and two wild species in Hokkaido (*D. ezoana* and *D.* sp. 4) are known as streamside dwellers. Therefore, two directions of the adaptive radiation are also seen in the *virilis* group. In Hokkaido, only one species (*D. pengi*) of the *melanica* group is known. According to TODA (1977) habitat of *D. pengi* is a forest canopy. Difference of habitat preferences between *D. pengi* and two forest dwellers of the *robusta* group (*D. sordidula* and *D. pseudosordidula*) may be important to reduce the interspecific competition.

From these, as shown in Fig. 11, it may be allowed to schematize the adaptive radiation of the three groups belonging to the old world *virilis-repleta* radiation in Hokkaido.

References

BEPPU, K., 1976. *Drosophila* Survey of Hokkaido, XXXI. Microdistribution of drosophilid flies

in the vicinity of the stream. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.*, **20**: 203–210.

———— 1978. *Drosophila* Survey of Hokkaido, XXXV. Further study on microdistribution of drosophilid flies in the vicinity of streams. *Ibid.*, **21**: 155–164.

BLIGHT, W. C., and A. ROMANO, 1953. Notes on a breeding site of *Drosophila americana* near St. Louis, Missouri. *Amer. Nat.*, **87**: 111–112.

CARSON, H. L., 1971. The ecology of *Drosophila* breeding sites. Harold L. LYON Arboretum Lecture Number **2**: 1–27.

DOBZHANSKY, Th., 1965. "Wild" and "domestic" species of *Drosophila*. *In* H. G. BAKER and G. L. STEBBINS (ed.), *The Genetics of Colonizing Species*, pp. 533–546. Academic Press, New York.

HERTING, B., 1955. Untersuchungen über die Ökologie der wildlebenden *Drosophila*-Arten Westfalens. *Z. Morph. u. Ökol. Tiere*, **44**: 1–42.

KANEKO, A., E. MOMMA, and T. SHIMA, 1967. Frequencies of abundance of *robusta* species group in Hokkaido. *Dro. Inform. Serv.*, **42**: 104.

————, ———— and T. TOKUMITSU, 1968. *Drosophila* collections in Hokkaido. *Proc. XII. Intern. Congr. Genet.*, **1**: 239.

———— and T. SHIMA, 1962. *Drosophila* Survey of Hokkaido, XVIII. Drosophilidae from four localities of Hokkaido. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.*, **15**: 74–79.

———— and H. TAKADA, 1966. *Drosophila* Survey of Hokkaido, XXI. Description of a new species, *Drosophila neokadai* sp. nov. (Diptera, Drosophilidae). *Annot. zool. Japon.*, **39**: 55–59.

———— and T. TOKUMITSU, 1969. *Drosophila* Survey of Hokkaido XXVII. On drosophilid flies from seven localities of the Hidaka district in southern Hokkaido. *J. Fac. Sci. Hokkaido Univ. Ser. VI. Zool.*, **17**: 244–256.

————, ———— and T. SHIMA, 1968. *Drosophila* Survey of Hokkaido, XXIV. On *Drosophila* collections of six localities in the southwestern part of Hokkaido. *Ibid.*, **16**: 531–536.

KIMURA, M. T., K. BEPPU, N. ICHIJÔ, and M. J. TODA, 1978. Bionomics of Drosophilidae (Diptera) in Hokkaido. II. *Drosophila testacea*. *Kontyû*, **46**: 585–595.

TAKADA, H., 1958 a. On the ecological characteristics of *D. ezoana* (*virilis* group). *Dro. Inform. Serv.*, **32**: 161.

TAKADA, H., 1958 b. *Drosophila* Survey of Hokkaido, X. Drosophilidae from several localities of Hokkaido. *J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.*, **14**: 120–127.

THROCKMORTON, L. H., 1975. The phylogeny, ecology, and geography of *Drosophila*. *In* R. C. KING (ed.), *Handbook of Genetics*, **3**: 421–469. Plenum Publ., New York.

TODA, M. J., 1973. Seasonal activity and microdistribution of drosophilid flies in Misumai in Sapporo. *J. Fac. Sci. Hokkaido Univ. Ser. VI. Zool.*, **18**: 532–550.

———— 1977. Vertical microdistribution of Drosophilidae (Diptera) within various forests in Hokkaido. I. Natural broad-leaved forest. *Jap. J. Ecol.*, **27**: 207–214.

———— and M. T. KIMURA, 1978. Bionomics of Drosophilidae (Diptera) in Hokkaido I. *Scaptomyza pallida* and *Drosophila nipponica*. *Kontyû*, **46**: 83–98.