Drosophila Survey of Hokkaido, XXXIV. Seasonal Variations of Body Color of *Drosophila testacea*

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(*With 6 Text Figures and 3 Tables*)

Natural populations of most species of *Drosophila* are remarkably uniform in external morphology. Therefore polymorphism, relatively common in many insects, is not a usual phenomenon as far as the outward appearance of *Drosophila* is concerned. Among the polymorphic species with regard to externally visible traits, color polymorphism has been found in some species of the genus *Drosophila*.

A marked color variation has been recorded on the abdomen of *Drosophila* (*Drosophila*) *testacea* van Roser (Burla and Gloor, 1953; Takada, 1960). This species has been captured as one of the most dominant species throughout all seasons in

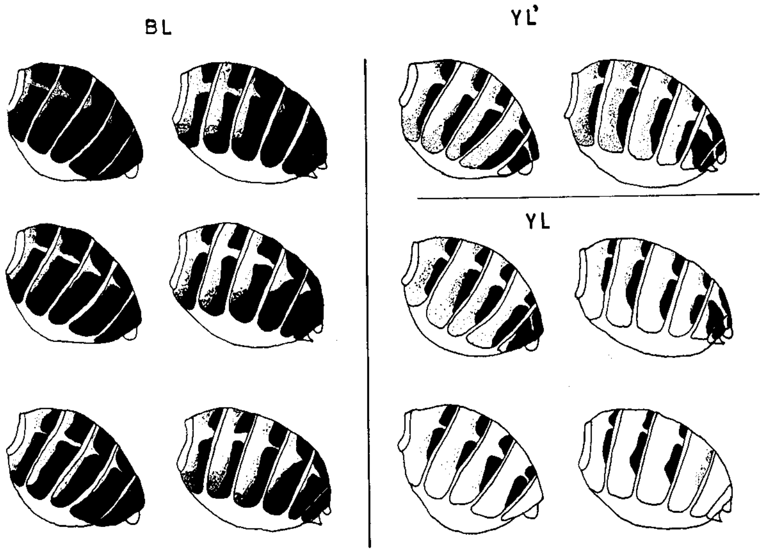

Fig. 1. Color patterns found on abdomens of *D. testacea* (cf. Takada 1960). Right, female; left, male.

Hokkaido. A rough classification of three color patterns was made (Fig. 1), and referred to as BL (black,), YL′ (brownish or reddish-yellow) and YL (yellow).

The present paper reports the results of a laboratory experiment on the color variation and of a survey of seasonal fluctuations of the color patterns in a natural population.

Before going further, the present author wishes to express his cordial thanks to Prof. Eizi Momma for his pertinent guidance in the course of this study and his reading of the manuscript. He is also grateful to Messrs. Masanori J. Toda, Masahito T. Kimura, Katsura Beppu and Naotaka Minami for their kind advıce and help in collection, and further to the Sapporo Meteorological Observatory for providing the meteorological data.

Area surveyed and collection method

To survey seasonal fluctuations of the different types in a natural population, flies were continuously collected throughout all seasons except winter in the Univeristy Botanical Garden. As the garden is located in the central area of Sapporo City, there would seem to be no immigration or emigration of the wild species from other fields' populations. The geography and vegetation of this area have been described by Momma (1965).

Two "retainer" traps (Toda *et al.*, 1975; Beppu and Toda, 1975) were set up

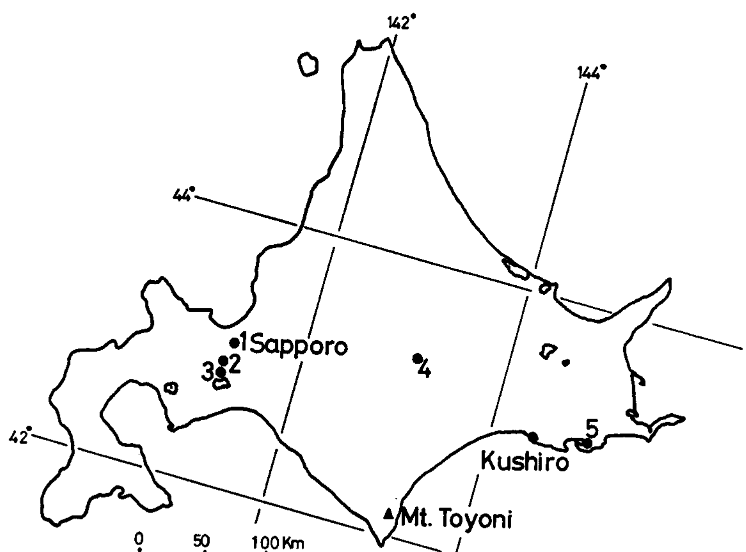

Fig. 2. Map showing collecting sites; 1, the Botanical Garden in Sapporo; 2, Mt. Sora-numa; 3, Mt. Eniwa; 4, Nukabira; 5, Akkeshi.

from April 21 to November 24 in 1975 and six traps from April 19 to November 22 in 1976. All the traps, baited with fermenting banana, were suspended from the branches or truncks of trees. Samples caught in the traps were removed every week. The samples were fixed with Kahle's solution. The reproductive condition of the wild-caught females was observed with the aim of better understanding the seasonal changes of the various types in relation to generation changes. For this purpose, four developmental stages of ovaries were classified (Watabe and Beppu, 1977).

These are Stage I, undeveloped; Stage II, developing; Stage III, mature; and Stage IV; postmature or degenerated ovary. The results obtained were recorded separately for the different types.

Experiment

Females captured in three localities near Sapporo (Fig. 2 and cf. Toda 1973) were placed in a vial, 3.0 cm in diameter and 10 cm in length. Offspring from females of the same color type were cultured from the egg stage at three different temperatures; 15°, 18° and 25°C. In the culture medium, mashed fungi (*Coprinus atramentarius*) were added. This medium was good for this species. The parent flies were turned out from the vial before their third instar larvae emerged, and the color patterns of the offspring were observed under a binocular microscope. Furthermore, crossing tests were carried out reciprocally between males and females originating from wild flies of the BL and YL types collected near Mt. Soranuma. Collecting data, culturing temperature, and results are summarized in Table 1.

Results

1. Seasonal fluctuation of the various types.

Of the total of 1416 specimens, 890 were collected in 1975 and 526 in 1976. The results obtained in the two years showed the same patterns (Fig. 3). The flies captured in spring showed distinctly black abdomens. After that, the black flies decreased in number. In summer the population was dominated by the yellow individuals. No fly of the BL type was collected in mid-summer. In fall, the black flies were obtained in large numbers again. The brownish or reddish-yellow flies were more frequently collected in late spring and early fall rather than in summer. The seasonal shift in color type suggested a temperature-induced response.

2. Life cycle and voltinism.

In general, this species showed a tetramodal seasonal activity with four main peaks in the Botanical Garden (Fig. 4). The first peak was in May, the second in late July, the third in late August and the fourth in October. The seasonal changes of female reproductive condition are demonstrated with absolute individuals numbers (Fig. 5). The fluctuation of male numbers corresponded with that of the females. Analysis of the field data has shown that this species has a multi-voltine life cycle in this area, because the females with undeveloped ovaries increased in number at least four times in a year. The first increase of undeveloped ovaries was recorded in early spring, the second in late July, the third in August and the fourth in October. The most noticeable feature is that most of the females collected in October, November and April showed Stage I ovaries. The ovaries are undeveloped over the winter. Such data suggest that *D. testacea* might, for the most part, have three generations in this area in a year.

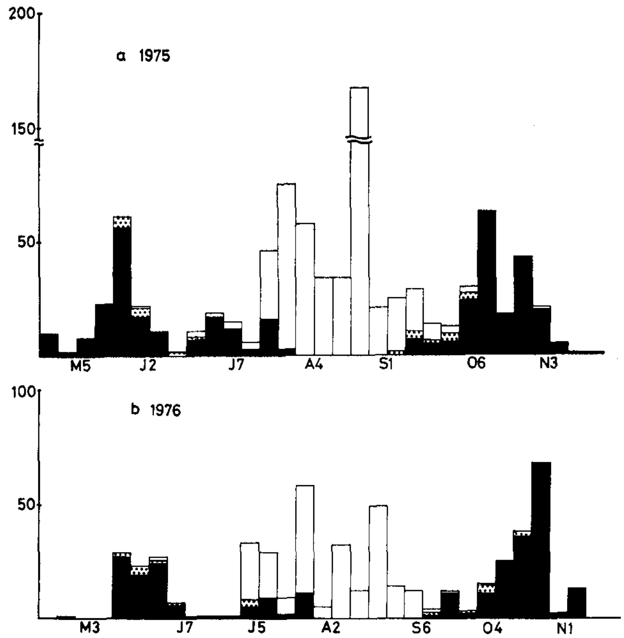

Fig. 3. Seasonal color fluctuations of BL, YL′ and YL types in the Botanical Garden. Black, BL; dots, YL′ and white, YL.

3. Results of experiment.

At a temperature of 25°C, the coloration of the progeny derived from both yellow and black wild flies was yellow without exception (Table 1). At 18°C, yellow flies were also obtained though the pigment area in the abdominal tergites spread to some extent, being brownish or reddish-yellow. In contrast, the black type was produced at the lowest temperature, 15°C. Crossing tests indicated that the color patterns in the offspring, irrespective of the color types of their parents, were light yellow in the 25°C culture and black in the 15°C.

Discussion

1. Genic and environmental polymorphism.

In brief, there are two general types of color variation in drosophilid flies. One is a genic variation, and the other depends upon environmental factors, temperature in particular. Heed (1963) termed the former "*genic polymorphism*" and the latter "*environmental polymorphism*" in some flies of the *cardini* species group.

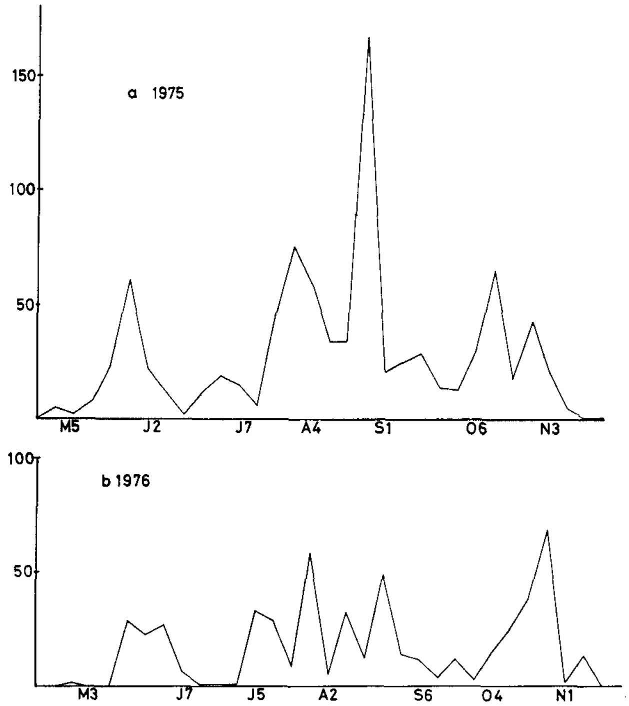

Fig. 4. Seasonal activities.

About seven polymorphic species of *Drosophila* as regards body coloration have been studied in detail. da Cunha (1946, 1949, 1953) established that three different color types of *D. polymorpha* in Brazil are controlled by two alleles. Heed and Blake (1963) reported a new color allele of the same species from northern South America. Females of *D. rufa* showed polymorphic patterns on the last two abdominal segments and this was due to two alleles (Oshima, 1952; Oshima and Taira, 1954). Polymorphic species of *D. l. lebanonensis* as regards mesonotal coloration are dependent upon a pair of color alleles (Pipkin, 1960). Polymorphic variation in *D. kikkawai* with regard to the coloration of the abdominal tergites, light and dark, is due principally to a single pair of autosomal genes (Freire-Maia, 1964). Two forms of the color patterns found in female *D. auraria* are produced by a set of allelic genes located on an autosome (Lee, 1964).

On the other hand, Stalker (1945) concluded on the basis of some experiments that color differences of *Scaptmyza graminum* (Drosophilidae) were mainly dependent upon the temperature. Sabath, *et al.* (1973) also reported that some color variations in *D. putrida* depended upon the temperature.

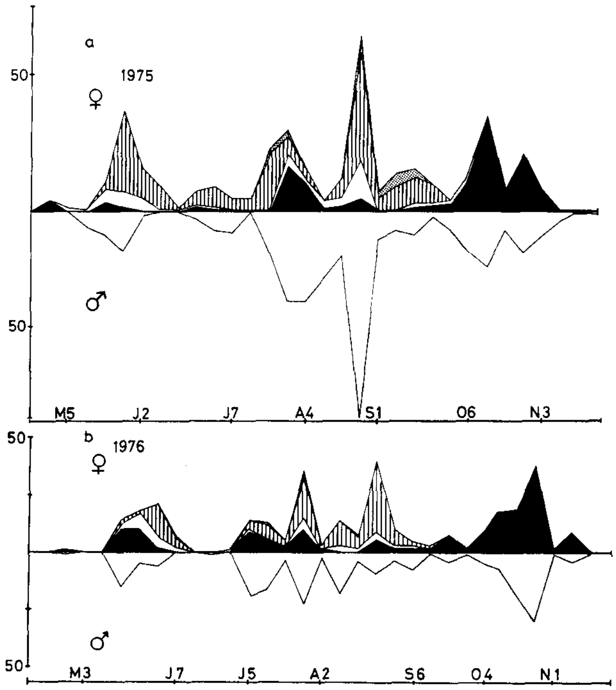

Fig. 5. Ovarian conditions during the season. Black, Stage I; white, Stage II; vertical lines, Stage III; dots, Stage IV.

Drosophila testacea is very close to *D. putrida* in phylogenetic relationship (Patterson and Stone 1952, Throckmorton 1975). The color patterns of this species resemble those of *D. polymorpha* according to da Cunha's figure (1949). But the phenotypical polymorphism of *D. testacea* depends not upon allelic genes but upon the temperature.

Takada (1960) reported that the color patterns of this species showed variations by altitudinal distribution on Mt. Toyoni, Hidaka Mountains, in August. The black flies were common at the higher altitude of 1100 meters and yellow at lower sites. Collections were carried out at Nukabira and Akkeshi (Fig. 2) in July 1975 and 1976, where the temperature during summer is very low (Table 2). The results of the collections are given in Table 3. The black flies in both areas were more abundant than in the Botanical Garden in the same periods. *Drosophila*

Table 1. Collection data, culturing temperature and the results of the laboratory experiments. (Further explanations in text.)

Collection data \ Color pattern	Parent	Progeny 15°C	Progeny 18°C	Progeny 25°C
Botanical Garden Sept. 23	YL	black 5	—	light yellow 18
Mt. Soranuma Sept. 1	YL	black 14	brownish or reddish yellow 13	light yellow 32
	BL	black 65	brownish or reddish yellow 13	light yellow 34
Mt. Eniwa	BL	black 60	brownish or reddish yellow 43	light yellow 31
Crosses (Soranuma strain)	BL♀ × YL♂	black 34	—	light yellow 39
	YL♀ × BL♂	black 30	—	light yellow 47

Table 2. Normals of monthly mean temperature from March to November (in °C, 1941–1970).

Locality \ Month	3	4	5	6	7	8	9	10	11
Sapporo	−0.6	6.1	11.8	15.7	20.2	21.7	16.9	10.4	3.7
Kushiro (near Akkeshi)	−2.1	3.2	7.7	11.4	15.4	17.9	15.2	9.6	3.3

testacea is very common in the northern hemisphere. It seems that the black flies are present through the season in the extreme northern population.

2. Seasonal fluctuation.

Little is known about the seasonal fluctuation of different color patterns in drosophilid flies (Sabath *et al.*, 1973). In the species under discussion, the seasonal color variations can be explained in relation to the changes of generation (Fig. 5 and 6). The females captured in early spring had undeveloped ovaries. The spring population represents the post-hibernated generation, passing the winter in the adult stage (Toda, personal communication 1976). This population is dominated by black individuals with a few of the brownish or reddish-yellow flies. The reproductive period of these flies is from late May to early July. The progeny (*first generation*) of the spring population appear in mid to late July. The abdomens of these flies growing in the ambient temperature (Table 2) were yellow. The ovaries of these flies develop rapidly. The offspring (*second generation*) of the yellow population appeared in early August and increased in late August, also showing the yellow pattern. The black flies of the spring population were not captured in mid summer.

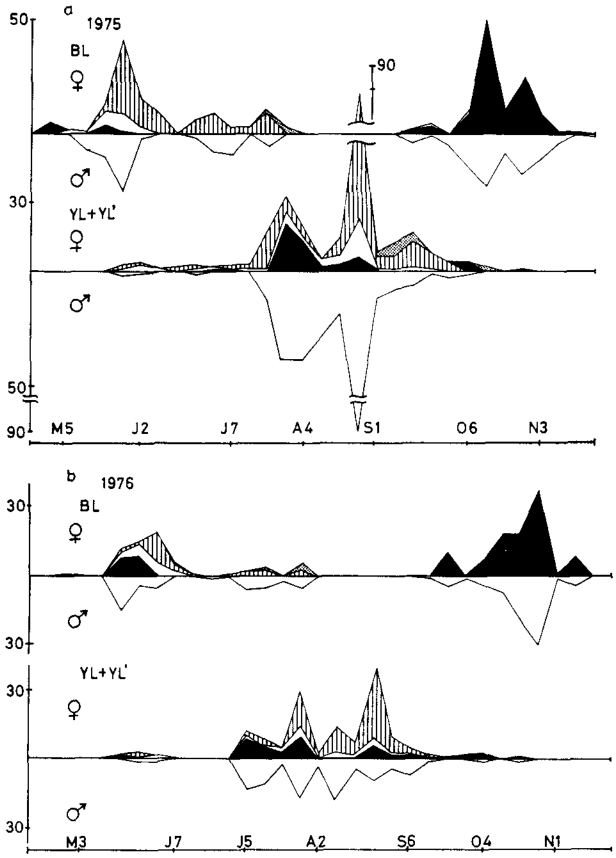

Fig. 6. The seasonal changes of the populations and ovarian conditions.

The reproductive period of the yellow flies of the second generation is from mid August to early September. The offspring (*third generation*) derived from these yellow types were the black type, being exposed to the low temperature in fall. The ovaries of the black flies do not develop between fall and the following spring. Therefore, the spring population represents the fall population of the previous year.

The brownish or reddish-yellow flies may be explained in two ways. First, they

Table 3. Color patterns and ovarian stages in two different populations.

Locality	Date	*C.P.	Ovarian stage				Male	Total
			I	II	III	IV		
Nukabria	July 1–3 1975	YL	—	—	—	—	—	0
		YL′	—	--	7	—	3	10
		BL	—	—	21	—	7	28
Akkeshi	July 2–8 1976	YL	2	—	2	—	7	11
		YL′	—	—	3	1	1	5
		BL	—	4	36	2	27	69

*C.P.; Color patterns.

hatch out in early fall. Second, they develop in comparatively warm breeding sites.

Summary

Body color variations were studied on *Drosophila testacea* in a natural population and in laboratory experiments.

1. Color variation was affected by the temperature during development. Flies raised at 15°C were more darkly pigmented than those raised at 18°C and 25°C.
2. In general, this species had three generations in the University Botanical Garden in a year. In spring and fall, the populations were dominated by black individuals which were replaced by yellow during summer months.
3. There was a relationship between the seasonal changes of the respective types and generation changes.

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