MIGRATION AND COMPETITION IN *DROSOPHILA*

II. EFFECT OF GENETIC BACKGROUND ON MIGRATORY BEHAVIOR OF *DROSOPHILA MELANOGASTER*

TAKASHI NARISE

Faculty of Science, Josai University, Sakado-Machi,
Saitama-Ken 350-02

Received August 13, 1969

In general, animals migrate or move from place to place to seek food and places in which to live or to leave their offspring. Consequently, migration or locomotion is an essential characteristic of animals, which is of great evolutionary and ecological importance. Recently, migration (or locomotion) was studied by Narise (1962) and Luchnikova (1966) with *Drosophila melanogaster* from the standpoint of behavior genetics, suggesting that migratory activity was a genetic character. Narise (1966, 1968) conducted experiments on migratory behavior of *D. melanogaster* and *D. ananassae* under genetically heterogeneous conditions. In these papers it was reported that the migratory activity of a strain was stimulated by other strain of the same species. For example, the activity of a vestigial strain of *D. melanogaster* increased when coexisting with a wild strain, and the same tendency was observed in a light type *ananassae* when the strain was mixed with the dark type. On the other hand, the wild type strain of *melanogaster* as well as the dark type of *ananassae* reduced its activity when mixed with alternate strains. These experimental results indicate that migratory activity of a strain is affected by other genetically different strains when they are mixed. Furthermore, it was revealed that the amount of change in the migratory activity of a strain depends upon the genotype of the coexisting strain. The average increment of the activity in light type *ananassae* from the Pago Pago population was 6.90% when the strain was mixed with the dark type *ananassae* from the Pago Pago population, while the increase was only 1.98% due to mixture with dark type from the Rarotonga. The purpose of this experiment is to examine in greater detail how migratory behavior of a strain of *Drosophila melanogaster* is affected by mixture with genetically different strains.

MATERIALS AND METHODS

The strains employed were five wild strains, MS-1, Niihama, Oshoro, Gifu and Tosu, and five vestigial strains derived from those five of *Drosophila melanogaster*. The wild type gene of those five wild strains was substituted by the vestigial gene. In addition to these strains, four F₁ hybrid strains between these wild ones were used.

The gene substitution was performed in the following way: one hundred virgin females of a vestigial strain were crossed with 100 randomly chosen males of a wild strain. One hundred virgin vestigial females from the F_2 generation were back-crossed to 100 males of the same wild strain as in the first cross, the same procedure of backcrossing being repeated ten times. In these crosses 100 males were used to minimize the loss, if any, of the inherent genetic variability of the wild strain. It may thus be expected that the genetic background of the vestigial strain finally obtained by such a procedure would be almost the same with the wild strain except for the vestigial locus. Hybridization was conducted among some of the wild strains to yield F_1 hybrids. Care was taken in this case to adopt 100 females from one strain and 100 males from the other to reduce the occurrence of random drift as far as possible. In order to measure the migratory activity of a wild or vestigial strain in a mixture, fifty flies of each strain were simultaneously introduced into a migration-tube (see Narise 1966). After 24 hours, three new tubes with fresh food were connected to it, and the flies in the newly connected tubes were counted and classified after six hours. The migratory activity of a strain was estimated on the basis of the number of emigrated flies in percent of initially introduced number of flies of the same strain. All experiments were conducted at $25 \pm 0.5^\circ \text{C}$ with no light except when counting or introducing flies. The experiment was replicated five times.

EXPERIMENTAL RESULTS

1) Interaction between genotypes in migration

Five wild strains, MS-1, Niihama, Oshoro, Gifu and Tosu, and their substituted vestigial strains were used. Each wild strain was mixed with each of the vestigial strains. The migratory activity of the wild strains is presented in Table 1. In this table, $vg(\text{MS-1})$ stands for the vestigial strain having the same genetic background as MS-1 wild strain, and so on, and "Alone" indicates the migratory activity of a wild strain inhabiting unmixed. In Table 1, it is found that the migratory activity of the MS-1 strain varied according to the genotype with which it is mixed: 13.2% in a mixture with $vg(\text{MS-1})$ was raised to 16.0% with $vg(\text{Tosu})$ and a similar increase in the

Table 1. Migratory activities of the five wild strains when mixed with different vestigial strains

Vestigial strain	Migratory activity of wild strains (%)				
	MS-1	Tosu	Gifu	Niihama	Oshoro
$vg(\text{MS-1})$	13.2	22.0	25.6	20.8	31.2
$vg(\text{Tosu})$	16.0	10.0	35.4	15.2	20.8
$vg(\text{Gifu})$	19.8	12.4	22.0	16.0	22.4
$vg(\text{Niihama})$	21.2	16.0	37.2	22.0	21.6
$vg(\text{Oshoro})$	20.8	13.2	27.2	19.2	19.6
Alone	26.8	28.4	21.6	28.8	24.6

migratory activity of the strain was again observed in combination with either *vg*(Gifu), *vg*(Niihama) or *vg*(Oshoro). It was also found in the same table that the migratory activity of the Tosu-strain in a mixture with *vg*(Tosu), Gifu with *vg*(Gifu) or Oshoro with *vg*(Oshoro) proved to be the lowest of different combinations. In other words, migration of a wild strain was the lowest when mixed with its substitution line of *vg*. The result of analysis of variance of the migratory activities of these wild strains in the mixed condition showed that there were highly significant differences between strains, between mixtures within strains and between "Alone" and mixed within strains ($p < 0.01$). The important finding from this experiment is that the migratory activity of each strain was stimulated in most cases positively, but seldom negatively, by strange genotypes coexisting with it.

Table 2 shows the migratory activity of vestigial strains when mixed with various wild strains. As seen in Table 2, 17.2% of *vg*(MS-1) showed migration when the strain

Table 2. Migratory activities of the five vestigial strains when mixed with different wild type strains

Wild strains	Migratory activity of vestigial strains (%)				
	<i>vg</i> (MS-1)	<i>vg</i> (Tosu)	<i>vg</i> (Gifu)	<i>vg</i> (Niihama)	<i>vg</i> (Oshoro)
MS-1	17.2	16.4	16.4	19.6	24.4
Tosu	23.6	11.6	16.4	12.0	20.0
Gifu	21.6	20.8	19.2	17.6	22.8
Niihama	18.8	27.6	16.8	8.0	18.8
Oshoro	24.8	14.4	18.8	15.6	13.6
Alone	11.0	11.0	18.8	5.8	13.4

was mixed with MS-1, while it became 23.6% in the mixture with Tosu strain. By combination with other wild strains the activity was also stimulated. In *vg*(Tosu), *vg*(Niihama) and *vg*(Oshoro) strains, a similar stimulation in positive direction was also observed in mixtures with wild strains, though in the case of *vg*(Gifu), it was reverse. From the result of analysis of variance of the migratory activity of the vestigial strains it was found that there were significant differences among strains, among mixtures within strains, and between mixed and unmixed within strains ($P < 0.05$). From the result of this experiment, it is clear that the migratory activity of vestigial strains was accelerated not only by its wild sister-strain having the same genetic background, but also by other wild strains involving different genetic background. It is concluded that the migration of a given genotype is affected by the genetic constitution of cohabiting strains, or the intensity of migration of a strain is more or less a function of the genetic effect of a strain cohabiting with it.

2) The relation between migratory activity and genetic similarity

In order to confirm the relation between migratory activity and genetic similarity of the mixed strains, experiments were conducted with MS-1, Niihama and Tosu wild strains, and four kinds of F_1 hybrids. In addition to these, *vg*(MS-1), *vg*(Oshoro) and

Table 3. Migratory activities of wild and vestigial type flies under the migratory condition

Combination			Migratory activity of	
wild type strain		vestigial strain	wild flies	vestigial flies
MS-1	+	<i>vg</i> (MS-1)	13.2%	17.2%
F ₁	+	<i>vg</i> (MS-1)	18.2	17.8
Niihama	+	<i>vg</i> (MS-1)	20.8	18.8
MS-1	+	<i>vg</i> (MS-1)	13.2	17.2
F ₁	+	<i>vg</i> (MS-1)	23.0	22.0
Oshoro	+	<i>vg</i> (MS-1)	31.2	24.8
Oshoro	+	<i>vg</i> (Oshoro)	19.6	13.6
F ₁	+	<i>vg</i> (Oshoro)	20.2	20.0
MS-1	+	<i>vg</i> (Oshoro)	20.8	24.4
MS-1	+	<i>vg</i> (MS-1)	13.2	17.2
F ₁	+	<i>vg</i> (MS-1)	17.6	20.4
Tosu	+	<i>vg</i> (MS-1)	22.0	23.6
Tosu	+	<i>vg</i> (Tosu)	10.0	11.6
F ₁	+	<i>vg</i> (Tosu)	13.2	14.0
MS-1	+	<i>vg</i> (Tosu)	16.0	16.4
Tosu	+	<i>vg</i> (Tosu)	10.0	11.6
F ₁	+	<i>vg</i> (Tosu)	15.0	13.0
Oshoro	+	<i>vg</i> (Tosu)	20.8	14.4
Oshoro	+	<i>vg</i> (Oshoro)	19.6	13.6
F ₁	+	<i>vg</i> (Oshoro)	16.8	17.6
Tosu	+	<i>vg</i> (Oshoro)	13.2	20.0

vg(Tosu) were used. The experimental results are presented in Table 3. The migratory activity of MS-1, Niihama and their F₁ flies was 13.2%, 20.8%, and 18.2%, respectively, when they were mixed with *vg*(MS-1). The activity of *vg*(MS-1) flies on the other hand, was 17.2%, 17.8% and 18.8% in mixtures with MS-1, F₁ and Niihama strain, respectively. As we know, the genetic background of *vg*(MS-1) is almost the same as that of MS-1 strain, while the genetic similarity between F₁ and *vg*(MS-1) strain is 50%. Needless to say, there is no similarity between Niihama and *vg*(MS-1). Thus, it is clear that the migratory activity of a strain, regardless it is wild or vestigial, increased when the opponent strains had different genetic backgrounds. The same was also seen in other combinations except for the cases of wild flies in Oshoro and Tosu combination. The result of analysis of variance of the migratory activity of wild as well as vestigial strains showed that there were highly significant differences between wild and vestigial strains ($P < 0.01$), as well as among different combinations within strains ($0.01 < P < 0.05$). This experimental result tells that migratory activity of flies is intensely affected by the genetic distance between strains inhabiting in a mixture.

DISCUSSION

Narise (1962, 1966, 1968) and Luchnikova (1966) have reported that migratory or locomotory activity of *Drosophila* was most certainly under genetic control. According to the two papers of Narise published in 1966 and 1968, the migratory activity of a strain was accelerated by the coexisting opponent strain which in turn decreased its

activity. The same was again found in the present experiment, data of which are given in Tables 1 and 2. However, a noteworthy phenomenon observed in this experiment was that the migratory activity of both wild and vestigial strains increased when the genetic backgrounds of the mixed strains are different. Furthermore, the activity seems to be accelerated by the genetic dissimilarity between mixed strains as presented in Table 3; the larger the difference between the genetic backgrounds of the two opponents in a mixture, the more intensive the migration of the flies occurs.

The other important problem is to what extent the migratory activity of a strain is affected by other strains. Let the average migratory activity of a strain when it was mixed with opponent strains having *different* genetic backgrounds be A and the migratory activity of the strain being mixed with the opponent having the *same* genetic background be B. Then the ratio A/B may take a value larger or smaller than or equal to unity. If the ratio is near unity, it means that the migratory behavior of the strain is little affected by different genotypes. As seen in Table 4, A/B ratios are quite

Table 4. The ratio of A to B in the wild as well as vestigial strains
(See text for explanation)

wild strains	A/B	vestigial strains	A/B
MS-1	1.47	<i>vg</i> (MS-1)	1.29
Tosu	1.59	<i>vg</i> (Tosu)	1.71
Gifu	1.43	<i>vg</i> (Gifu)	0.89
Niihama	0.81	<i>vg</i> (Niihama)	2.03
Oshoro	1.22	<i>vg</i> (Oshoro)	1.58

variable among strains, indicating that the effect of foreign genotypes on migratory activity is apparently different among strains. The A/B ratio of Tosu showed the highest value among wild strains, while among vestigials, *vg*(Niihama) was the highest. The migratory behavior of these strains seems to be most easily affected by different strains.

SUMMARY

Experiments were conducted to estimate the migratory behavior of *D. melanogaster* under the genetically heterogeneous conditions. Five wild, five vestigial and four kinds of F₁ hybrid strains between wild strains were used.

The migratory activity of the vestigial strains was promoted by the wild ones except in a few cases, while the wild type strains were reduced in activity when mixed with vestigial strains. Furthermore, the migratory activity of either wild type or vestigial strains increased when mixed with strains of different genetic background.

From the results of cross-experiment, it was found that the larger the difference between genetic background of the two strains in a mixture, the more intense the stimulation effect on migratory activity appears.

ACKNOWLEDGMENTS

The author wishes to thank Dr. Kan-Ichi Sakai, the head of the Department of Applied Genetics, National Institute of Genetics, Mishima, for valuable comments and suggestions. The author is also indebted to Dr. Richard C. Lewontin, Department of Biology, University of Chicago, for his critical reading of the manuscript and comments. This work was carried out in the National Institute of Genetics when the author was the research member of the Institute.

LITERATURE CITED

- Luchnikov, E. M., 1966 Character of genotypical differentiation of the level of general locomotive motion activity of *Drosophila melanogaster*. (Russian with English summary) *Genetika* **5**: 36-46.
- Narise, T., 1962 Studies on competition in plants and animals, X. Genetic variability of migratory activity in natural populations of *Drosophila melanogaster*. *Japan. J. Genetics* **37**: 451-461.
- Narise, T., 1966 The mode of migration of *Drosophila ananassae* under competitive condition. *Univ. of Texas Publ.* 6615: 121-130.
- Narise, T., 1968 Migration and competition in *Drosophila* I. Competition between wild and vestigial strains of *Drosophila melanogaster* in a cage and migration-tube population. *Evolution* **22**: 301-306.