IX. NOTE ON GENE VARIABILITY IN NATURAL POPULATIONS OF DROSOPHILA

MARY L. ALEXANDER

INTRODUCTION

The present investigation was designed to determine the comparative frequency of mutations in natural populations of two different species of Drosophila. The cosmopolitan species, *Drosophila hydei* Sturtevant (1921), occurs as both domestic and wild populations but *Drosophila macrospina limpiensis* Mainland (1941) is found only as isolated or semi-isolated wild populations in a restricted distribution area. The genetic variability of these two species is compared in as far as such variability is reflected in the mutant frequencies.

Material and Methods

The stocks for this investigation were obtained by field collections from natural populations. Most collections from Arizona, Utah, and New Mexico were made at suitable ecological habitats in the desert area along streams which flow through canyons and oases. Both species were obtained from this area whereas only *D. hydei* was obtained from eastern collections. The eastern area extends from South Carolina north to New Hampshire, and west to Wisconsin, Illinois, and Ohio. The populations within this area were collected in a wild habitat except two collections which were in picnic grounds. Tables 1 and 2 give the collection location of the strains used.

Supplementary tests were made with a lethal and mutant free strain of *hydei,* stock 1758.1a which was collected at Grand Fork, North Dakota, July 24, 1947, and stock 1223.7a of *limpiensis* which was collected at Zion National Park, Utah, August 3, 1941.

Tests for Mutants

The F_1 progeny from flies collected from natural populations were checked for visible mutations and inbred in pairs. This method was modified since the two species which were tested differ in fecundity, fertility, breeding habitats, and other physiological features. The P_1 individuals of *limpiensis* were mated in pairs. The F_1's from a pair were checked for visible mutations and mated in pairs to recover autosomal recessive mutations. A maximum number of twenty F_1 pair matings were made to compensate for any loss due to unsatisfactory test; ten F_2 pairs were checked from each F_1 pair for visible mutations whenever possible. The detection of lethals in *limpiensis* by means of egg counts was found to be impracticable since the fertilized females produce some eggs containing sperm and others without sperm. The low egg hatch of 10–20 per cent is at least partially due to this defect in fertilization.

In *hydei* the F_1 generation was obtained from isolated females which had been fertilized in nature, from pair matings, or by crossing a male or unfertile female of the natural population to the test stock, 1758.1a. The F_1 flies from a pair mating or an isolated female were checked for visible mutations and mated in pairs. The number of F_1 pairs checked varied somewhat as shown in Tables 1 and 2. Lethal tests were made from a suitable sample in some cases. Egg counts were obtained from P_1 crosses when pair matings were used and autosomal recessive lethals were detected by egg counts on the F_1 pairs.

RESULTS

Table 1 gives the number of P_1 individuals tested from each locality, the number of F_1 pairs tested, and the distribution of mutants in *hydei* populations. All mutants recovered from the F_1 or F_2 generation are recorded under *Mutants Recovered;* mutants recovered in subsequent generations are placed under the heading of F_3 *Mutants.* The presence of phenocopies is indicated by plus signs. A comparable arrangement of data for *limpiensis* is given in Table 2 except for F_3 mutants. The mutants were arranged according to the structure effected as wing mutants, eye colors, or wing veins.

The total number of mutations for each species was determined on the assumption that morphologically similar and even allelic mutants from different populations are different mutations—that is, originated as independent mutations. The average number of mutants per fly was obtained by a comparison of the number of mutations recovered from the F_1, F_2, and F_3 generations with the P_1's, counting the P_1 pair as two individuals and the unfertile female or tested male as one. Averages for isolated females were made on the basis that the offspring came from the last male which fertilized the female in nature.

A comparison between Tables 1 and 2 show that a great many more phenocopies occurred in *limpiensis* than in *hydei.* A total number of 19 major mutations were found in *limpiensis* and 79 in *hydei.* The average number of mutations per fly was 2.38 for *hydei* and 1.14 for *limpiensis.*

A large number of eye color mutants of different types were found in *hydei* populations. There was a consistent difference between several of the mutants from the time of emergence. Others appeared similar on emergence but darkened at different rates. Therefore different names in the table of mutants usually refer to different mutants or alleles.

In contrast to the non-allelic mutants, *striped,* a body pigmentation, can be classified as a species-wide mutant. It was recovered from twelve of the fifteen localities and eight of these different mutants tested proved to be allelic. These came from stocks 1870.7, 1854.10, 1907.6, 1881.5, 1873.6, and 1897.17. Although some quantitative differences in morphological expression existed between different stocks, *striped* was easily recognized in all offspring in these tests.

TABLE 1: MUTANT DISTRIBUTION IN DROSOPHILA HYDEI

Stock Number	Location	Pl's Tested	F_1 Pairs	Mutants Recovered: Eye Color	Abnormal Abdomen	Thorax Pattern	Body Color	Lethals	Semi-lethal	Wing Mutants	Vein Mutants	Facets Irregular	Bristle Mutants	Size Mutants	F_3 Mutants: Wing Mutants	Leg Mutants	Phenocopies: Dark Pigment	Shaven	Mottled
1868.5	Flagstaff, Arizona	a (pair)	10	red	a.a.			autosomal	s.l.	reduced	delta, cross-veinless						+		+
		b(♂×S♀ *)	7	red	a.a.			no test			delta							+	
1870.7	Payson, Arizona	a (pair)	5	rose	a.a.			autosomal											+
		b (pair)	10	rose	a.a.	pale		sex-linked					bobbed						
		c (pair)	11	rose	a.a.	pale	striped	autosomal				rough	bobbed				+	+	+
1854.10	Patagonia, Arizona	a (pair)	5	carmine				autosomal		taxi			minute, hooked		spread-duplicated throax	tarsus short			
		b (pair)	8	carmine	a.a.	pale		autosomal			delta						+		
1873.6	New Mexico	a(♀×S♂ *)	0	bright	a.a.	pale	striped	autosomal										+	+
1877.12	S. Carolina	a (pair)	1	bright		pale	striped	no test											
1878.3	N. Carolina	a (iso ♀)	5	bright		pale	striped	no test			delta	rough		small			+		
		b (iso ♀)	1	bright		pale	striped	no test							snipped				
1881.5	Virginia	a (iso ♀)	1			pale	striped	no test					bobbed						
1889.10	N. H.	a (iso ♀)	1	bright	a.a.	pale	striped	no test											
1897.17	New York	a (pair)	8	red	a.a.	pale	striped	none	s.l.				bobbed				+		
1899.14	Ohio	a (iso ♀)	3			pale	striped	no test											
1901.4	Jackson, Michigan	a (iso ♀)	3	bright	a.a.	pale		no test									+	+	
		b (pair)	4	bright	a.a.	pale		no test					bobbed						
1904.6	Menominee, Michigan	a (pair)	8	bright	a.a.	pale	striped	no test											
1905.4	Wisconsin	a(♀×S♂ *)	6			pale	striped	none											+
1907.6	Carlinville Illinois	a (iso ♀)	7	bright	a.a.	pale	striped	no test		burnt			bobbed				+		
		b (iso ♀)	12	bright	a.a.	pale	striped	autosomal							curled			+	+
		c (iso ♀)	9	bright	a.a.	pale	striped	no test											
1909.5	Carlinville Illinois	a (iso ♀)	5	orange	a.a.	pale		no test		spread				dumpy					
		b (pair)	4	orange	a.a.		striped	no test											

* Laboratory Strain 1758.1a

TABLE 2

Mutant Distribution in Drosophila Macrospina Limpiensis

Stock Number	P_1 Pair	F_1 Pairs	Mutants Recovered					Phenocopies					
			Mottled	Semi-lethal	Eye Color	Bristle Mutants	Size Mutants	Spread Wings	Twisted Wings	Shaven	No Crossvein	Rough Eye	Droopy Wings
1865.2	a	11	mottled	s. l.				+	+				
Veyo, Utah	b	8	mottled	s. l.					+	+			
	c	4		s. l.		extra							
	d	4	mottled	s. l.					+				
1868.4	a	4	mottled					+				+	+
Flagstaff, Arizona	b	1	mottled										
	c	1	mottled										
1870.3	a	10	mottled	s. l.		double	dumpy	+	+		+		
Payson, Arizona	b	11	mottled	s. l.					+				
	c	8	mottled	s. l.				+	+		+		
1853.4	a	8	mottled						+				
Idlewild Forest Camp, Arizona	b	5							+				
	c	7	mottled			thread (F_3)		+	+	+		+	
	d	6	mottled							+		+	
1854.1	a	6	mottled	s. l.	cherry, scarlet			+					
Patagonia, Arizona	b	4	mottled	s. l.	cherry						+	+	
	c	7	mottled	s. l.	cherry, scarlet, peach			+	+				
	d	9	mottled	s. l.	scarlet			+	+	+			
	e	7	mottled	s. l.	cherry, scarlet, peach	dumpy						+	
1850.8	a	10	mottled	s. l.		extra		+	+	+	+	+	+
Big Bend, Texas	b	9	mottled	s. l.					+	+		+	+

Allelic mutants similar to *bobbed* which was first described by Clausen (1923) was recovered from five different localities. Further investigations of *hydei* populations by Spencer (1927, 1944) established the proof of a diverse series of allelic *bobbed* mutants. At least two alleles at the *bobbed* locus were present in the 1897.17, 1901.4, and 1881.5 stock since isolated females gave two types of *bobbed* females when crossed to a strong *bobbed* test male (stock 1870.7). Although such *bobbed* mutants are usually recessive, a dominant or semi-dominant action was exhibited by some strains in the F_1 females when tested against the lethal-mutant free strain 1758.1a. Males are of normal phenotype except for the occasional appearance of sterile *bobbed* males in some strains, as *bobbed*-1881.5, 1897.17, and 1901.4. Crossing-over between the X and Y in the male or the elimination of the Y giving an XO type male could explain such cases. Such quantitative interactions are rather complicated and obviously several different alleles are involved to give the different interactions found.

No allele test was carried out on the *lethal, abnormal abdomen* or *pale* mutants. Lethal mutants were found in five of the nine strains tested. Although most lethals were autosomal recessive, one sex-linked recessive lethal was found in the P_1 and F_1 generation of 1870.7. The *pale* mutants offered difficulty in allele test since classification is not possible except in aged flies. The *abnormal abdomen* mutants were so low in viability that allele test were very difficult.

Allele test have not been completed for *limpiensis* mutants. The dominant or semi-dominant *mottled* mutants occurred in such low frequency when first recovered that allele test were impracticable. A pure strain of *mottled*-1865.2 has now been obtained and the frequency of morphological expression has been increased in most other strains. The bristle mutants *extra*-1865.2 and *extra*-1850.8 have not been tested for allelism since strains with constant expression have not been established.

DISCUSSION

Such mutant variability as that found in this investigation shows that gene mutations occur and are retained within the natural populations of two species with quite different population distribution and structure. Along with such major differences as visible mutations, many minor mutations as well as variations dependent upon multiple gene action undoubtedly occur, but detection and isolation of such factors are very difficult.

One characteristic of both species is the occurrence of morphological similar mutants which are widespread throughout the distribution area. Spencer (1947) has reported such mutants in several other species of Drosophila. The different *mottled* mutants of *limpiensis* and the *striped* and *bobbed* mutants of *hydei* showed differences in intensity and frequency of expression. Minor genetic variations produced by recombination of genes within different populations or different quantitative levels of the gene may account for such diverse minor expressions. Retention of such mutants may depend upon the instability of certain loci with high

mutation rates, upon neutral selective advantage, or, as the case may be in *bobbed,* upon an effective mechanism which reduces selective action.

The mutation variability within *limpiensis* populations consisted primarily in one type of widespread mutant, *mottled,* with very few recessive mutants except in the 1854.1 sample. The *hydei* populations contained more species-wide mutants and showed greater recessive variability which is distributed in a somewhat mosaic pattern.

The study of the dynamics of evolution in natural populations by use of mutant variability is very incomplete at the present time. In *D. melanogaster* studies, H. A. and N. W. Timofeeff-Ressovsky (1927) recovered 10 different mutant types from a Berlin sample of 78 females which had been fertilized in nature. The mutant variability was limited to a high incident of a few mutants. Two sex-linked lethals were also recovered from this small sample. N. P. Dubinin and co-workers (see Spencer, 1947) found a high incident of a widely distributed mutant, *trident,* in Russian populations of *melanogaster.* Although a larger sample than that of the Berlin populations was used, no sex-linked lethals were found. Spencer (1947) recovered 20 visible mutations from 408 long chromosomes tested (Ohio populations) whereas Dubinin and associates recovered only 34 from a sample of Gelendzhik populations in which more than 10 times more chromosomes were tested. Such discrepancy of results in these studies of different *melanogaster* populations can always be explained by difference of testing methods or sampling error but it is also possible that the populations of these three localities have quite different structure.

Nine lethals, a high incident of a *small bristle* mutant, and a fairly large number of different visible mutations were found in Texas populations of *D. virilis* by Patterson, Stone, and Griffen (1942). Although a limited sample was tested, the presence of mutant variability in *virilis* populations is shown. *Drosophila limpiensis* is a species which had not been previously investigated for mutation structure but Mainland (unpublished) obtained mutants from natural populations and X-ray material.

Even from these limited studies it is apparent that considerable genetic variability, as exemplified by easily detectable visible mutants, is characteristic of a number of Drosophila species. There exists, in addition, an extensive series of lethals of a fairly appreciable frequency as shown by studies with *D. pseudoobscura* (Dobzhansky, 1939, and Dobzhansky and Wright, 1941).

Mutants with effects too small to be determined consistently are probably much more numerous than those with more obvious effects. The genetic picture is one of populations that contain individuals each with several diverse alleles.

REFERENCES

Clausen, R. E. 1923. Inheritance in *Drosophila hydei.* American Naturalist 57:52–58.

Dobzhansky, Th. 1939. Genetics of Natural Populations. IV. Mexican and Guatemalan Populations of *Drosophila pseudoobscura.* Genetics, 24:391–412.

Dobzhansky, Th., and Sewall Wright. 1941. Genetics of Natural Populations. V. Relations Between Mutation Rate and Accumulation of Lethals in Populations of *Drosophila pseudoobscura*. Genetics, 26:23–51.

Patterson, J. T., Stone, Wilson S., and Griffen, A. B. 1942. Genetic and Cytological Analysis of the Virilis Species Group. The University of Texas Publication, 4228:162–183.

Spencer, W. P. 1927. The X Chromosome of *Drosophila hydei*. Journal of Experimental Zoology, 47:441–446.

Spencer, W. P. 1944. Iso-alleles at the Bobbed Locus in *Drosophila hydei* Populations. Genetics, 29:520–536.

Spencer, W. P. 1947. Mutations in Wild Populations in Drosophila. Advances in Genetics, Vol. 1:359–402.

Timofeeff-Ressovsky, H. A., and N. W. 1927. Genetische Analyse Einer Freilebenden *Drosophila melanogaster* Population. Archiv. fur Entwicklungsmechanik der Organism, 109:70–109.