MESONOTAL COLOR POLYMORPHISM IN DROSOPHILA L. LEBANONENSIS[1]

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BALANCED color polymorphisms in the genus Drosophila have been found in the *cardini*, *virilis*, and *melanica* groups of the subgenus Drosophila and in the *melanogaster* group of the subgenus Sophophora. The present work is a long-term study of laboratory cage populations prepared from strains derived from natural populations exhibiting a monogenic mesonotal color polymorphism occurring in *D. l. lebanonensis*, of the *victoria* group of the subgenus Pholadoris. Light mesonotum was found to be dependent on an autosomal gene, *S;* dark mesonotum, on its allele, *s* (PIPKIN 1956, 1961). The purpose of the work is to compare the progress of a monogenic polymorphism in population cages with that of chromosomal polymorphism studied by others with respect to (1) formation of equilibria, (2) dependence upon the composition of the initial population, (3) influence on early generations of heterosis caused by using strains of different geographical regions.

Natural polymorphic populations of *D. l. lebanonensis* have been found in Jerusalem, Israel, and in the following localities in The Lebanon: two coastal regions (Beirut and Byblos), six mountain collecting stations (Asfouriye, Ain Anub, Ainab, Sofar, Torzaya, and Azouniye), and in the Bekaa Valley (Ksara and Chtaura). A map showing the Lebanese localities was given by PIPKIN 1952. *D. lebanonensis*, WHEELER 1949, was described from dark specimens before the polymorphism was recognized. In view of the large number of collections made (PIPKIN 1952), it is believed that the infrequency of *D. l. lebanonensis* in traps indicates that the species exists in small populations. Two related sap-feeding Nearctic species, *D. brooksae* and *D. victoria*, which are known to be averse to entering fruit-baited traps, are cultured with difficulty on laboratory medium. *D. l. lebanonensis* populations showed slight but typical expansion in spring fruiting months at two collection localities and breeds well in mass culture on cornmeal medium.

The data on the frequencies of the color forms of *D. l. lebanonensis* in natural populations are unfortunately incomplete; however, it is clear that a balanced trimorphism of color forms exists in natural populations. Some of the flies taken at each of the six regular collecting stations must have been heterozygous for the pair of color alleles (*S*, light; *s*, dark mesonotum), since both light and dark

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homozygous strains were subsequently isolated from collections made at each of these localities. Notes in original collection books list some specimens "much paler than the usual light form." These are believed to have been homozygotes, *SS*. Table 1 gives the frequencies of color forms recorded.

MATERIALS

Polymorphic strains of *D. l. lebanonensis* from four Lebanese localities were carried in culture vials until 1954, the homozygous dark strain from Ain Anub having been established soon after collection. At this time, the Beirut strain showed 54 percent dark and 46 percent light forms (PIPKIN 1956). Subsequently, strains homozygous for *S* (the light allele) or for *s* (the dark allele) were isolated by single male, single female crosses from polymorphic strains of each locality (except in the case of the homozygous dark strain of Ain Anub). Several such similar cultures were pooled to prepare strains for use in population cage experiments. Stocks available for use in 1959 included homozygous *SS* light strains from Beirut and Rasco (Jerusalem), and *ss* dark strains from Ain Anub and Ksara.

Description of the character: In stock strains homozygous for the light allele *S*, from Beirut or from Rasco, the mesonotum is yellowish tan posterior to the level of the anterior dorsocentral bristles. Anterior to this level the mesonotum is brown with a median pale stripe extending anteriorly to the vertex and two lateral pale paramedian stripes extending to the suture. The scutellum is yellowish with paramedian brown stripes. *SS* individuals of the Beirut and Rasco strains show very little variation in color. Within the *ss* dark strains of Ain Anub and Ksara, there is a slight variation in intensity of thoracic color, which is chestnut brown in some individuals, darker brown in others.

F_1 hybrids between homozygous light and dark strains are uniformly colored. They are, with rare exceptions to be noted shortly, dark from the anterior end of the thorax to the level of the anterior dorsocentral bristles. From this point posteriorly, the mesonotum is yellowish tan to the scutellum which is dark brown,

TABLE 1

Frequencies of color forms in natural populations of D. l. lebanonensis

Locality	Year	Light	Dark
Ain Anub	1947	16	5
Ain Anub	1948	11	6
Azouniye	1947	8	0
Beirut	1947–48	9	1
Sofar	1948	14	1
Chtaura	1948	4	0
Ksara	1948	2	2
Ainab	1947	1	2
Total		65	17
Percent		79.27	20.73

medially and yellowish, laterally. Flies were placed head facing the observer when being scored. All scoring was done by the author.

RESULTS

Demonstration of monogenic inheritance: The P_1 cross of light homozygotes, *SS*, with dark homozygotes, *ss*, produced only light progeny, regardless of the strains used, according to Table 2. The *Ss* heterozygote progeny of the P_1 cross displayed a uniform "hybrid light" phenotype previously described, with the following exceptions: Five males and one female of the cross between the Rasco and Ksara strains and eight offspring of the cross between the Beirut and Ain Anub strains showed a thin median pale streak anterior to the anterior dorsocentral bristles. Thus *Ss* rarely can be confused with *SS* even in F_1 *Ss* heterozygotes derived from strain crosses.

The backcross of *Ss* heterozygotes with *ss* homozygotes gave approximately equal numbers of light and dark progeny according to Table 2.

In the corresponding backcross, *Ss* × *SS*, there is evidence that recessive modifier(s) in the Beirut strain altered the dominance relationship between *S* and *s* in the pale direction. When *Ss* males of the strain composition Ain Anub/Ksara / Beirut were backcrossed to *SS* Beirut females, the *SS* and *Ss* progeny could not be separated phenotypically. Nearly all these offspring possessed the median and lateral pale streaks characteristic of *SS* progeny. The pale dominance modifiers must be located on a chromosome not homologous with the *S* chromosome since they were effective in heterozygous *Ss* progeny of the backcross. Single male tests are difficult to carry out in this species even though three transfers of the original test to fresh food vials were made. However, 54 such backcross male progeny, tested individually, proved to be *Ss*; 43 were *SS*. If a single light backcross male offspring crossed with six dark *ss* females produced a progeny segregating approximately 50 percent light, 50 percent dark, the genotype of the male being tested was concluded to be *Ss*. If the single light backcross male offspring

TABLE 2

Demonstration of monogenic inheritance

P_1 cross *SS*		*ss*	Progeny F_1 light (*Ss*)		
Beirut/Rasco	×	Ain Anub/Ksara	152		
Beirut	×	Ain Anub/Ksara	230		
Beirut	×	Ain Anub	1,393		
Rasco	×	Ksara	207		
Backcross *Ss*	×	*ss*	light (*Ss*)	dark (*ss*)	Chi-square and P
Beirut/Ain Anub/Ksara	×	Ain Anub	351	333	0.4736 0.5<P<0.3
Beirut/Ain Anub	×	Ain Anub	913	903	0.05506 0.9<P<0.8

crossed with six dark *ss* females produced all pale progeny, the genotype of the male being tested was concluded to be *SS*.

When two different *SS* strains, i.e., Rasco and Beirut, were used in the backcross, the phenotypes of both *SS* and *Ss* progeny could be identified. Thus, of the backcross Rasco/Ain Anub (*Ss*) × Beirut (*SS*), a total of 336 individuals were scored as *Ss* and 648, as *SS*. Hence, the Rasco and Beirut strains must differ somewhat in respect to the pale modifiers.

F_2 ratios of the cross Beirut/Ain Anub (*Ss*) males with similar *Ss* females carried out in three different half-gallon bottles were scored as follows: 48 *SS*, 137 *Ss*, 23 *ss*; 25 *SS*, 195 *Ss*, 64 *ss*; 27 *SS*, 145 *Ss*, 38 *ss*. In crosses of the strain composition Beirut/Ain Anub/Ksara (*Ss*) males × females of the same genotype, carried out in half-pint bottles, the following progeny were scored: 46 *SS*, 308 *Ss*, and 69 *ss*.

Cytology: Salivary gland preparations of *D. l. lebanonensis* show chromosomes with three long arms, two medium length arms, and two short arms. The chromocenter is pronounced. One gland is larger than the other, an observation made by WHARTON (in WHEELER 1949), who first studied the chromosomes of this species. Among 25 single larva aceto-orcein preparations of the Ain Anub (*ss*) strain, one short inversion was found. No inversions were found in 14 single larva preparations of the Ksara strain (*ss*). Of *Ss* heterozygotes, no inversions were present in 48 single larva preparations arising from the cross of the Ain Anub (*ss*) and Beirut (*SS*) strains, in 12 larvae of the composition Rasco/Ksara, or in 19 larvae of composition Rasco/Ain Anub. Thus a total of 79 single larva preparations of the genotype *Ss* showed no inversions. No lack of pairing of chromosome parts was found in any of these *Ss* heterozygotes. In contrast, PIPKIN (1961) found a partial or complete lack of pairing in one or both arms of the medium length chromosome in half the preparations as well as two different inversions in other chromosomes of some of the preparations of hybrids of *D. l. lebanonensis* and *D. l. casteeli*.

Design of cage experiments: A photograph of a population cage used in these studies, with dimensions indicated, is given in Figure 1. Of a modified DA CUNHA-BURLA design, the cornmeal culture medium was contained in quart-sized Mason jars attached horizontally to the central stainless steel adult resting chamber. Two lateral faces and a bottom circular panel made of fine screen, afforded ventilation. In this species, egg to hatching time was 24 days under laboratory conditions. A sample of 400 flies was counted and scored every 29 to 30 days when most of the individuals were four to six days old, and body color well-formed. In addition to this sample, all other flies possible to extract by phototropism from the old cage were each generation placed in a clean cage provided with three Mason jars containing fresh food. A fourth jar was added shortly after flies began to emerge in order to provide food while the flies were aging so that their color could be scored. Discrete generations were studied. Soon after the second generation in each population cage the total number of flies in cages reached a level of between two and three thousand per generation. The populations were cultured at temperatures of 21° to 23°C, relative humidities of 55

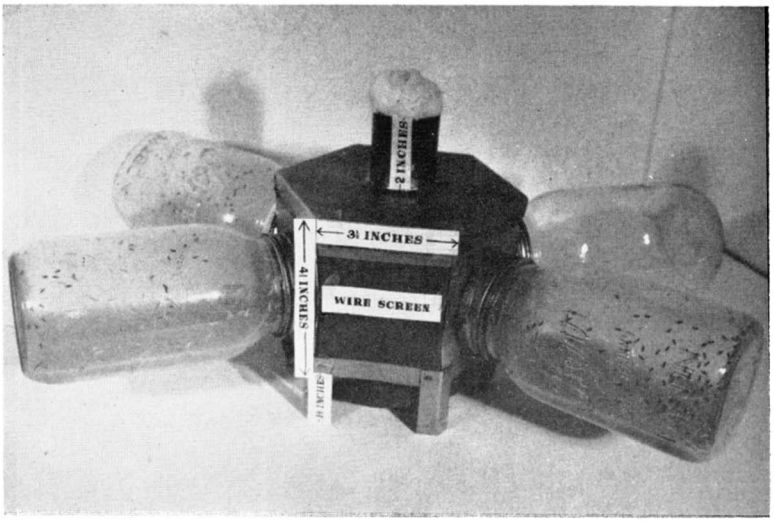

FIGURE 1.—Photograph of the population cage (by DR. ALAN C. PIPKIN).

percent to 60 percent, closely approximating the temperatures and humidities of natural populations of this species (PIPKIN 1952).

The experimental populations were of three general designs. Those of design I were begun with equal proportions of homozygous light, *SS*, and homozygous dark, *ss*, males and females. Design II populations were begun with 20 percent homozygous light, *SS*, and 80 percent homozygous dark, *ss*, males and females. The initial populations of cages of design III were composed of *Ss* strain hybrids. The strain compositions and initial population sizes are given in Table 3. Cage populations were carried varying lengths of time from six to 28 generations. Genotypic tests of individual male samples taken from several generations of each of the various cage populations were made by crossing one male with six homozygous *ss* females of the Ain Anub or Ksara strains, as described previously

TABLE 3

Designs of cage populations

Design	Initial proportion	Initial population size	Cage no.	Strain composition
I.	50% *SS*	100	1a, 1b, 1c,	Beirut (*SS*)
	50% *ss*	200	3a, 3c	Ain Anub/Ksara hybrids (*ss*)
			7a, 7b, 9a	
II.	20% *SS*	100	2a, 2b	Beirut (*SS*)
	80% *ss*	200	8a, 8b	Ain Anub/Ksara hybrids (*ss*)
III.	100% *Ss*	200	11a, 11b	Beirut/Ain Anub hybrid males and females (*Ss*)
			12a	Rasco/Ain Anub/Ksara (*Ss*)
			10b	Beirut/Rasco/Ain Anub/Ksara (*Ss*)

for tests of backcross progeny. Since the maturation period is only two days in this species, the males had already mated when withdrawn from the population for scoring. Scored females were returned to the cages.

Results of cage experiments: Graphs showing the percentages of *SS*, *Ss*, and *ss* individuals in certain type I cage populations are presented in Figure 2; in type II populations, in Figure 3; and type III populations in Figure 4. (Graphs of populations 1a, 1b, 1c, 7a, 3c, 2a, 2b, and 11a are placed on file with the editor together with tables showing the percentages of *SS*, *Ss*, and *ss*, as scored phenotypically in various generations of certain cage populations.) Heavy lines represent frequencies of phenotypes; i.e., of individuals scored $SS(p)$, with median stripe anterior to the level of the dorsocentral bristles; $Ss(p)$, with mesonotum dark anterior to this level; and $ss(p)$, with mesonotum dark throughout. Dashed lines represent frequencies of genotypes $SS(g)$, $Ss(g)$, and $ss(g)$ obtained from testing individual males of various generations. The number of successful tests in early generations of the cage populations, when the effects of strain heterosis were apparent, was higher than in later generations. Owing to the number of unsuccessful tests, percentages of genotypes of the three classes which belong to any generation, n, were plotted as belonging to generation $n + 1$. In a few cases, the genotypic frequencies of two successive generations were pooled. The genotypic and phenotypic percentage curves of the same population differ due to (1) errors of sampling, (2) the presence of recessive modifying gene(s) which affect the phenotypic expression of *SS*, *Ss*, and *ss* individuals so as to cause mistakes in scoring. In the first two generations of populations 1a, 1b, 1c, 3a, 3c, 2b, 8a, and 8b, the *Ss* and *SS* classes were not separated phenotypically. However, the *SS* class must have been absent or occurred in very low frequency during the first two generations as may be seen from populations 7b, 9a, (and 2a) where these classes were separated, beginning with the first generation.

The percentages of *SS*, *Ss*, and *ss* individuals followed a somewhat different course in the three types of populations studied. A lesser degree of variation occurred within populations of the same design. According to Figure 2, there was a beginning period of heterozygote (*Ss*) superiority lasting from ten generations in population 3a to 18 generations in population 7b in type I populations. The period of heterozygote superiority was longer in type II populations, ranging from ten generations in population 2b to 28 generations in population 8b. The beginning of the decline in frequency of *Ss* heterozygotes occurred from generation 7 in population 9a to generation 13 in population 7b in type I populations and from generations 7 to 9 in type III populations. The *Ss* heterozygotes have an advantage in type I populations, beginning with the first generation, owing to strain heterosis resulting from the crossing of Beirut (*SS*) and Ain Anub/Ksara (*ss*) parents. The *ss* homozygotes in type I populations enjoyed a secondary advantage since the *ss* parents used to start the cage populations were hybrids between the Ain Anub and the Ksara *ss* strains.

The *ss* homozygotes were sustained at approximately the frequency of the first generation for from two to nine generations in type I populations and for

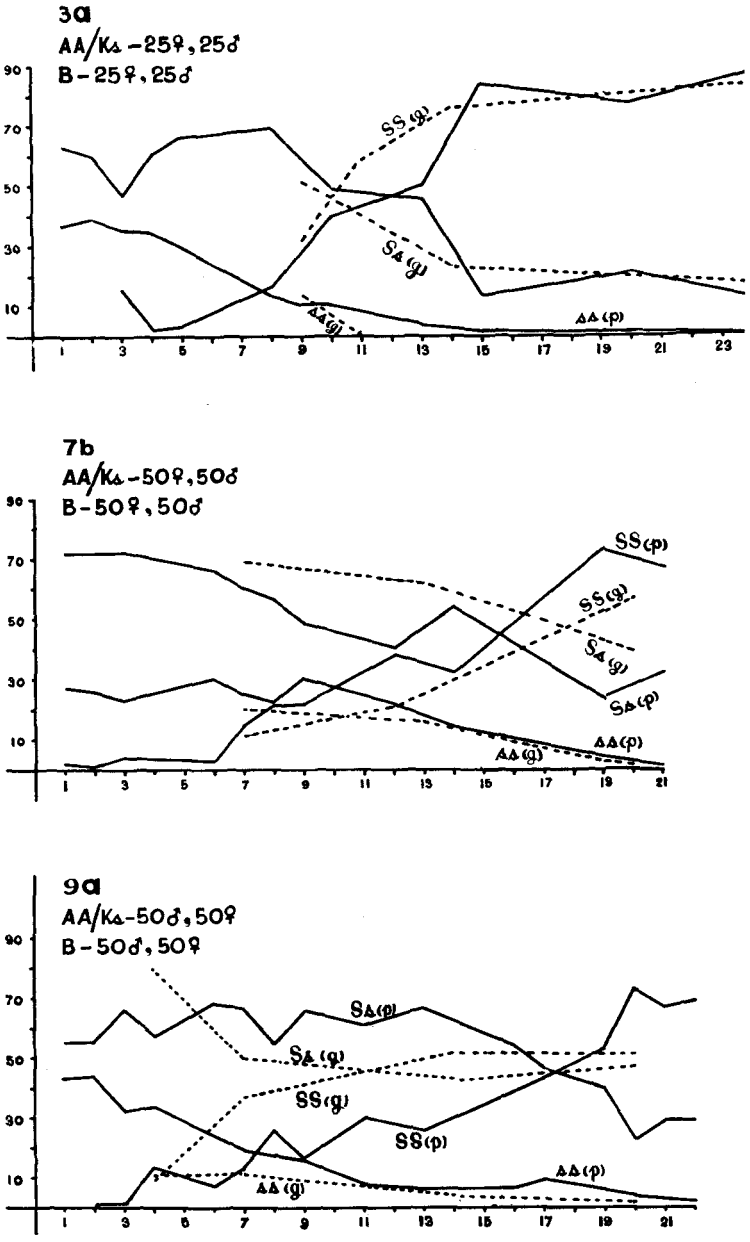

FIGURE 2.—Percentages of *SS*, *Ss*, and *ss* individuals in type I populations. Generation number is plotted along the abscissa. Solid lines represent percentages derived from scoring phenotypes of these groups. Dashed lines represent percentages derived from testing male samples genotypically.

eight generations in type II populations before a continuous decline in the frequency of this group began. The *ss* class was lowest in type III populations, and

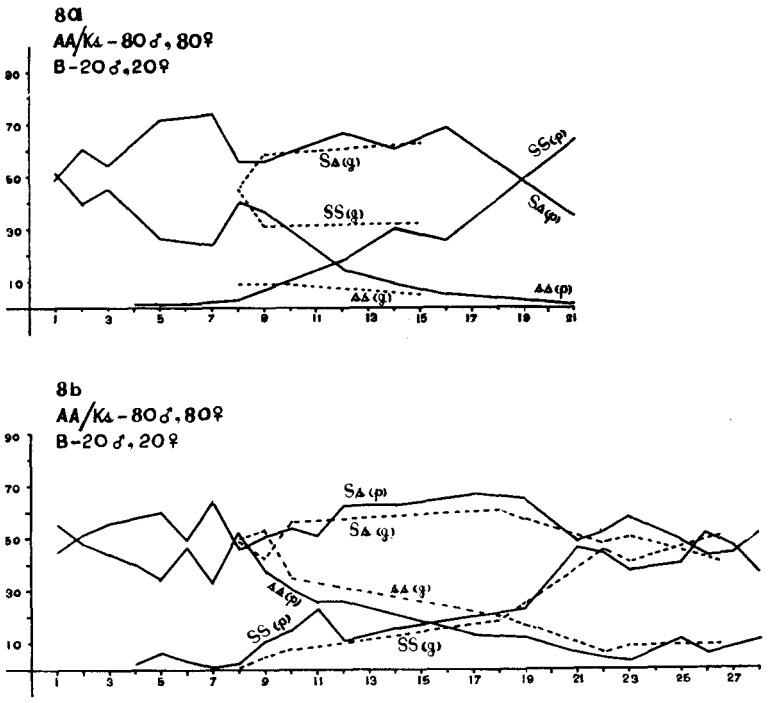

FIGURE 3.—Percentages of *SS*, *Ss*, and *ss* individuals in type II populations.

there was a continuous decline in the group from the second and third generations on.

Homozygous *SS* flies were either absent or in very low frequency according both to phenotypic scoring and to genotypic tests of male samples in the first and early generations of the eight type I and four type II populations studied. On the basis of random mating and absence of differential fecundity of parent groups and viability of progeny, *SS* homozygotes were expected to constitute 25 percent of the first generation of type I populations where equal numbers of *SS* and *ss* males and females formed the initial groups. It is thought that the *SS* female parents must be less fecund and/or the *SS* homozygote progeny must suffer in larval and pupal competition during the first generation since *SS* homozygotes arise from the crossing within the same Beirut strain, whereas both *Ss* and *ss* progeny are derived from three or two strains, respectively. The fact that a sizable number of *SS* homozygotes occurred in the first generation of type III populations, which were composed initially of *Ss* heterozygous males and females, is explained by the absence of such single strain *vs.* strain hybrid viability differences. A rise in the frequency of *SS* homozygotes was continuous though not as regular as the corresponding decline of *ss* frequency in populations of all three designs, regardless of whether the *S* allele was derived from the Beirut or from the Rasco strain. The ascent in frequency of *SS* homozygotes occurred earlier in type III than in type I and type II populations.

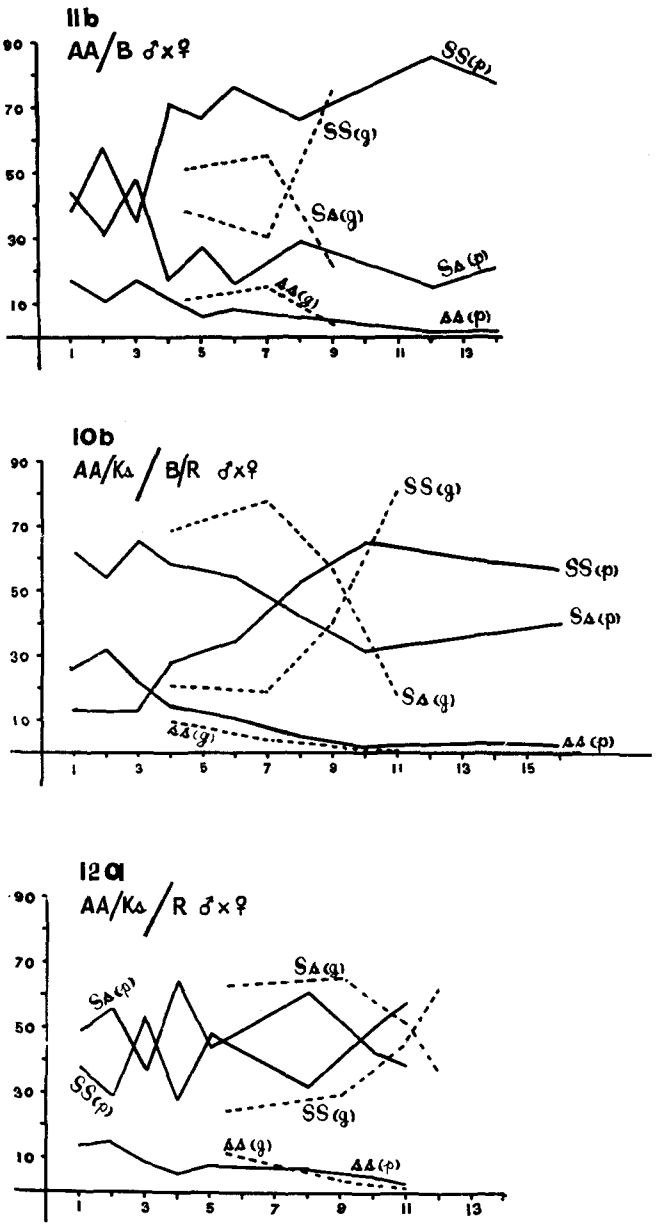

FIGURE 4.—Percentages of *SS*, *Ss*, and *ss* individuals in type III populations.

Recessive modifiers: Errors in scoring *SS*, *Ss*, and *ss* phenotypes of well-aged flies are thought to be due chiefly to genetic modifiers. As shown previously, the variation in expressivity of *Ss* heterozygotes in F_1 offspring of *SS* and *ss* strains is slight. Little variation of phenotype occurs within the *SS* and *ss* strains. Modi-

fiers segregating in cage populations may alter the phenotype of *Ss* heterozygotes either in a light or in a dark direction, the phenotypes of *ss* homozygotes in a light direction, and the phenotype of *SS* homozygotes in a dark direction.

Table 4 gives data resulting from genotypic tests of individual males coming from various populations of design I. [Data resulting from genotypic tests of males coming from populations of designs II and III are placed on file with the editor.] The leftmost column contains the number of the population to the left; the number of the generation to the right. Thus "3c 6" means that the males tested came from the sixth generation of population 3c. According to Table 4, 549 males scored *Ss* proved by individual male tests to be genotypically *Ss* as scored. On the other hand, 146 males scored *Ss* proved to be genotypically *SS*; 31 males, scored *Ss* proved to be genotypically *ss*. Two hundred and seventeen males scored *SS* proved to be *SS* according to genotypic tests; but 36 males scored *SS* turned out to be *Ss* genotypically. One hundred and ninety-three males scored *ss* proved to have *ss* genotypes, but 49 males scored *ss* were *Ss* according to the the genotypic tests. Genetic modifiers in a light direction are particularly noticeable in the type III population 11b and from generation 4 through generation 9 in population 10b, according to Figure 4. In population 9a, modifiers buffered

TABLE 4

Tests of individual males of various generations of type I populations

Gen. tested	Scored *Ss*; tested *Ss*	Scored *Ss*; tested *SS*	Scored *Ss*; tested *ss*	Scored *SS*; tested *SS*	Scored *SS*; tested *Ss*	Scored *ss*; tested *ss*	Scored *ss*; tested *Ss*	Total
3c3	61	4	0	23	5	22	4	119
3c6	97	8	2	15	10	12	2	146
3c10	4	6	0	7	1	1	0	19
3c11	17	22	0	3	0	0	1	43
3a8	30	13	0	9	0	10	6	68
3a10	15	9	0	13	0	0	0	37
3a13	4	1	0	16	3	0	0	24
3a15	0	8	0	10	0	0	4	22
3a23	2	0	0	19	0	0	0	21
1a7	16	3	4	0	0	36	2	61
1c6	56	6	11	7	0	32	0	112
1c7	22	5	4	8	1	19	3	62
7a5	0	0	0	2	0	8	0	10
7a10	48	7	0	4	0	13	0	72
7b6	19	4	0	0	0	8	4	35
7b12	22	2	0	6	1	6	0	37
7b19	14	2	0	30	8	2	0	56
9a2	58	6	10	2	0	9	0	85
9a6	32	34	0	7	3	14	20	110
9a8	3	0	0	5	0	0	3	11
9a13	10	5	0	7	0	0	0	22
9a18	6	0	0	0	0	0	0	6
9a19	13	1	0	24	4	1	0	43
Totals	549	146	31	217	36	193	49	1,221

the phenotypic changes in frequencies of *SS* and *Ss* genotypes since Figure 2 shows that the decrease of $Ss(p)$ and corresponding increase of $SS(p)$ is more gradual than the decline of *Ss* genotypes ($Ss(g)$) and rise of *SS* genotypes ($SS(g)$). In population 9a, the genotype *SS* was modified phenotypically in a dark direction from generations 7 to 17. From generations 17 to 21, the *Ss* genotype was modified in a light direction. Similarly, Figure 4 shows that in later generations of population 10b the genotypic curves of $SS(g)$ and $Ss(g)$ differ more widely from one another than do these groups according to phenotypic classification. On the other hand, Figure 3 indicates that in later generations of populations 8a and 8b, the genotypic frequencies $SS(g)$, $Ss(g)$, and $ss(g)$ closely approximate the corresponding phenotypic frequencies, $SS(p)$, $Ss(p)$, and $ss(p)$.

Polymorphism in D. brooksae: A light and dark mesonotal polymorphism occurs in *D. brooksae* (PIPKIN 1961), similar to that studied in *D. l. lebanonensis*. In *D. brooksae,* the entire mesonotum is pale in the light form. At the time of collection, in May, 1960, by DR. W. B. HEED (personal communication), an estimated 60–70 percent of the specimens were black or dark brown; 30–40 percent, light brown (HEED, personal communication). Flies were not etherized at this time since they were known to be difficult to carry on laboratory medium. Three generations after the collection in nature, a sample of a bottle population included 92 black or dark brown (78%) and 25 (21.3%) light brown. The frequencies of color forms are exactly reversed from the situation in natural populations of *D. l. lebanonensis* where Table 1 shows 79.3 percent light; 20.7 percent dark. After culturing *D. brooksae* without selection for 19 generations from the time of the original collection, a sample proved to contain 88 dark (49.72%) and 89 (50.28%) light yellowish tan flies. Thus the mesonotal polymorphism in this species has changed in laboratory bottle populations in the direction of lightness. Further there is evidence of recessive modifiers since the "light" color of *D. brooksae* in nature is nevertheless distinctly darker than the "light" group in laboratory populations carried for 19 generations.

DISCUSSION

Trimorphism of mesonotal color in laboratory cage populations of *D. l. lebanonensis* was shifted strongly in the direction of dimorphism, approaching monomorphism in populations 3a, 11a, and 11b. A clear-cut equilibrium of frequencies of *SS*, *Ss*, and *ss* genotypes occurred from generations 23 through 28 in population 8b, and suggested equilibria between the *SS* and *Ss* genotypes occurred in the 21st and 22nd generations of populations 8a and 9a. Thus heterosis of heterozygotes for the single pair of alleles responsible for mesonotal color polymorphism, which is balanced in natural populations, is dependent not upon overdominance at a single locus but upon selection of a specific genetic background just as DOBZHANSKY (1950) found in the case of heterosis of hybrids for certain gene arrangements in *D. pseudoobscura* cage populations initially composed of strains derived from geographically different regions.

In the present study, cage selection during the beginning period was stabilizing, favoring an approximation to the F_1 strain hybrid genotype, or, with respect to the mesonotum character, *Ss*. From the second to the seventh generations, cage selection began to be directional, favoring *SS* homozygotes, and continued to operate until arrested by the establishment of equilibria in certain populations. THODAY (1960), using *D. melanogaster*, showed that recombination of marker genes is far higher when a stabilizing selection (for a mean sternopleural chaeta number), in contrast with a disruptive selection, is practiced in a line begun with hybrids between two parental lines characterized by "high" and "low" sternopleural chaeta number, respectively. An important function of strain heterosis in the small natural populations of *D. l. lebanonensis*, occurring in a mountainous area, may be to favor recombination. STONE, ALEXANDER and CLAYTON (1954) showed that in *D. novamexicana*, F_1 strain hybrids placed for four months in population cages underwent rapid selective changes in certain fitness changes measured.

The pattern of changes in *D. l. lebanonensis* mesonotal polymorphism in cage populations carried for a sufficiently long time shows a dependence upon the composition of the initial groups. First, the color trimorphism was shifted more rapidly toward dimorphism and monomorphism, with *SS* homozygotes replacing the other genotypes, in type III populations where *SS* homozygotes occurred in sizable numbers in the first generation than in type I or II populations where this group was virtually absent in the first generation. Secondly, the effect of the presence of heterotic *ss* strain hybrids in initial populations of designs I and II was to prolong the trimorphism by bolstering the selective advantage of the *ss* and *Ss* groups. This influence was more pronounced in type II populations which were started with 80 percent *ss* strain hybrids and 20 percent *SS* homozygotes of the single Beirut strain, particularly in populations 8a and 8b, each of which was begun with 200 parents, compared with populations 2a and 2b, in which the parents used to start each cage numbered 100. To a lesser extent, this bolstering of the selective advantage of the *Ss* heterozygotes also may be seen in the type III population 12a, begun with *Ss* heterozygotes derived from the crossing of the Rasco strain (*SS*) with *ss* homozygotes which were themselves hybrids of the Ain Anub and Ksara strains. The shift toward monomorphism was strongest in the two strain type III populations 11a and 11b, where no bolstering by strain heterosis of the selective values of the *ss* group took place. Similarly, the selective value of certain inversion heterozygotes in *D. pseudoobscura* (LEVENE, PAVLOVSKY and DOBZHANSKY 1954, 1958) and in *D. persimilis* (SPIESS 1961) has been found to depend on the frequencies of other karyotypes present in the respective beginning cage populations.

Previous investigators working with monogenic color polymorphisms not associated with inversions have reported a balanced polymorphism dependent on heterozygote superiority in cage populations (DA CUNHA 1949; FREIRE-MAIA 1949; OSHIMA and TAIRA 1956). The present work shows that equilibria are not established in cage populations of *D. l. lebanonensis* before the 21st generation. In *D. polymorpha* where cage populations were carried only six generations,

DA CUNHA (1949) contrasted the superiority of *Ee* heterozygotes in most of his cage populations with the fact that in all 14 natural Brazilian populations studied, the frequencies of homozygotes *EE* and *ee* were higher than expected on the binominal square rule. HEED (1961) postulated the existence of a third allele at the *e* locus to account for DA CUNHA's discrepancy. Since the *D. polymorpha* cage populations were begun with several light and several dark strains derived from different geographical localities, the heterozygote group would be expected to be high owing to the influence of strain heterosis during the first six generations. The homozygote groups might have shown an increase in frequency if the cage populations had been carried longer.

Why did the mesonotal color polymorphism prove potentially transient in several *D. l. lebanonensis* cage populations in contrast with the balanced condition in natural populations? The superior fitness character(s) possessed by *Ss* heterozygotes of natural populations were eventually lost by *Ss* heterozygotes of most cage populations initiated from strains of different geographical localities since integrated gene complexes were to a varying extent broken up by recombination in strain hybrids. DOBZHANSKY and PAVLOVSKY (1958) found that the inversion superiority of more than 50 percent in natural populations of *D. paulistorum* and *D. willistoni* is maintained in cage populations only if the latter originated from single geographical strains. BRNCIC (1961) obtained similar results with *D. pavani*. However, CARSON (1961) found that a population of *D. robusta* begun with strain hybrids not only maintained the inversion polymorphisms of the respective strains but actually accepted a new inversion polymorphism. Inversion polymorphism, with reduction of crossing-over both within and to some extent without the limits of the inversion(s) would be expected to be more effective in preserving the components of genetic systems than monogenic phenotypic polymorphism in species with free crossing-over.

Secondly, environmental differences doubtless affected the selective values of genotypes belonging to the *D. l. lebanonensis* color polymorphism in laboratory *vs.* natural populations. Population cages provided a food source, a ventilated resting area, protection from the uncontrolled rigors of predators, competitors, mold, bacterial infection, or temperature change. In natural populations of *D. l. lebanonensis* there is a winter diapause in the mountain localities studied (PIPKIN 1952). In addition, the difference in population size in *D. l. lebanonensis* natural *vs.* cage populations constitutes an important environmental difference between the two.

LEWONTIN (1957) concluded that if the environment is constant, a heterotic polymorphic system must eventually break down and be replaced by a monomorphic one. The same author suggested that the shift from polymorphism to monomorphism should be demonstrable in the laboratory (LEWONTIN 1958). BUZZATI-TRAVERSO (1952) had anticipated these ideas when he stated that the requirements of a constant environment are better met by populations that genetically are less diversified. Inasmuch as the *D. l. lebanonensis* cage populations were constructed from strains of several different localities, the influence of a constant environment on the nature of the polymorphism cannot be separated

from the influence of using mixed strains. The shift toward monomorphism in *D. brooksae* may depend on factors other than a constant environment (e.g., drift, since the species was cultured in half-pint bottles), but at least the observed change suggests that the question of the effect of a constant environment on a monogenic polymorphism is not settled. SCHNICK, MUKAI and BURDICK (1960) found that the equilibrium frequency of heterozygotes for the lethal *l(2)55i* changed from about 0.42 to 0.20 in a period of from 16 to 40 generations in the laboratory, a change which may depend in part on the selective effect of a constant environment. In the case of chromosomal polymorphism, on the other hand, CARSON (1961) found only rare inversions to be lost from populations of *D. robusta* carried 30 generations in the laboratory. He suggested that LEWONTIN's hypothesis holds only under those conditions in which each heterozygote is specially adapted in nature to some slightly different environmental variable which is not repeated in the laboratory. LEVINE and BEARDMORE (1959) and SPIESS (1961) concluded that a constant environment does not necessarily prevent the maintenance of chromosomal polymorphism in long term experiments.

The degree to which the change in the character of the polymorphism found in cage populations of *D. l. lebanonensis*, in comparison with the trimorphism of natural populations, may be dependent upon the change in the system of mating in cages is uncertain. MATHER (1955) pointed out that inbreeding forms will produce homozygous genotypes to become balanced by natural selection in contrast with the largely heterozygous genotypes produced by normally outbreeding forms. The degree of inbreeding in cage populations is probably not sufficient to affect the polymorphism since CARSON (1961) found no difference in "mean population fitness" as measured by total population weight developed on a given amount of culture medium in a *D. robusta* "open" population compared with a "closed" one.

Modifiers both in the light and dark directions of the *SS*, *Ss*, and *ss* phenotypes in *D. l. lebanonensis*, causing errors in scoring phenotypes of cage populations and in the progeny of the *Ss* × *SS* backcross are reminiscent of those described by FORD (1954) in the progeny of strain hybrids of *Triphaena comes*. As in the latter, there is evidence that the *D. l. lebanonensis* "pale" modifiers are not identical (or at least not in the same frequency) in the Rasco and Beirut strains. The modifiers in *D. l. lebanonensis* illustrate dominance as a special case of epistasis since the phenotypes of heterozygotes, *Ss*, as well as of homozygotes, *SS* and *ss*, are altered so as to cause errors in scoring. These modifiers could be described as homeostatic in certain populations where they buffered phenotypic changes in comparison with the genotypic changes known to have occurred from tests of male samples.

SUMMARY

The monogenic mesonotal color trimorphism in *D. l. lebanonensis* was shifted to dimorphism and in the direction of monomorphism in laboratory cage populations initially composed either of homozygous dark (*ss*) and homozygous light (*SS*) strains or of hybrids between such light and dark strains, derived from

originally trimorphic populations of different geographical localities. *SS* homozygotes eventually had the highest selective value in all cage populations except one in which a clear-cut equilibrium between the frequencies of *SS*, *Ss*, and *ss* genotypes developed. Apparently the *Ss* superiority in early cage populations due to strain heterosis breaks down in most cage populations owing to recombination. The trimorphism was prolonged in cage populations begun with 80 percent *ss* and 20 percent *SS* parents compared with populations begun with equal numbers of *SS* and *ss* individuals, showing dependence upon the frequencies of these genotypes in initial populations. The shift toward monomorphism was strongest in cage populations begun with *Ss* parents, hybrids of a single homozygous light and a single homozygous dark strain. The effect of strain heterosis on early generations of certain cage populations was to prolong the period of trimorphism. Modifiers both in a light and in a dark direction caused errors in scoring *SS*, *Ss*, and *ss* phenotypes in cage populations so as to make necessary testing of individual males from cage populations. These modifiers could be considered homeostatic since they caused less drastic phenotypic changes compared with genotypic changes in certain populations. A monogenic mesonotal polymorphism in the *victoria* group species, *D. brooksae*, is also described.

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