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CORRELATIONS BETWEEN EGG PRODUCTION AND CHROMOSOMAL REGIONS IN DROSOPHILA MELANOGASTER

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Abstract

Correlations of daily egg production in Drosophila melanogaster with the segments, sc cv and v f of the first chromosome and with the segments, al dp and b pr of the second chromosome were investigated for the two genetic backgrounds, Oregon-R and M Oregon-R. The results show that large intrachromosomal effects and interactions do exist with their magnitudes being largely dependent on background and chromosome. Evidence is also cited to suggest that recombination is also influencing the trait.

A small experiment in predictability was performed and a reasonable degree of success was achieved.

CORRELATIONS BETWEEN EGG PRODUCTION AND CHROMOSOMAL REGIONS IN DROSOPHILA MELANOGASTER[1]

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Introduction

Egg production in Drosophila melanogaster is an inherited trait and the existence of strains which differ in their egg production (Gowen and Johnson, 1946; Bonnier, 1961; Keller and Mitchell, 1964; Chapco, 1965) is sufficient proof of this fact. Inheritance implies chromosomal activity and it has been established that all three major chromosomes influence the character (Straus, 1952; Robertson and Reeve, 1955; and Keller and Mitchell, 1964). In his analysis of data obtained by Karp (1940), Gilbert (1961) studied the influence of parts of chromosomes on egg production. However, from a 'factorial design standpoint', the data were incomplete and therefore a thorough analysis of the fractional replicate to obtain main effects and interactions was not undertaken.

The main objective of this study is to investigate the effects on egg production of two segments of the X-chromosome and two segments of the second chromosome. This will be done on two genetic backgrounds whose effects will be compared. As a matter of interest and an exercise in predictability, the effect on fecundity of two chromosomal segments in combination is compared with a predicted value based on the sum of their individual contributions.

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Materials and Methods

Two wild-type strains, Oregon-R (designated as A) and M Oregon-R (designated as D) and two mutant strains, sc cv v f and al dp b pr were employed in this work. The first mutant strain carries the four sex-linked markers: sc (scute bristles), cv (crossveinless), v (vermilion eyes), and f (forked bristles). These occupy the respective positions: 0.0, 13.7, 33.0, and 56.7 on the first chromosome. The al dp b pr strain is marked by the four genes: al (aristaless), dp (dumpy wings), b (black body), and pr (purple eyes). These occupy the respective locations: 0.0, 13.0, 48.5, and 54.5 on the second chromosome. The A and D strains were obtained from Dr. L. Butler at the University of Toronto in 1965 as highly inbred stocks, the previous histories of which are recorded by Seiger (1966). The two mutant strains were obtained from the Carolina Biological Supply Company in 1965 as mass cultured stocks. The two wild-type strains were chosen for their large fecundities and were used to provide genetical backgrounds for the less fecund mutant strains. Another reason for employing the latter stocks was that the segments, sc cv, v f, al dp and b pr could be regarded as integrated units and their effects on egg production studied. The positions of the markers are such that the occurence of a double crossover within each segment is expected to be infrequent.

All crosses were single-pair matings. Each of the two marker stocks was placed on A and D backgrounds by repeatedly backcrossing, in alternate generations, each of sc cv v f and al dp b pr segregating females to A and D males. This resulted in the creation of the four tester stocks, sc cv v f (A), sc cv v f (D), al dp b pr (A), and al dp b pr (D) with the genetic background indicated in parentheses; the number of backcrossing steps were ten, eight, ten and eight, respectively. The unmarked chromosomes of each tester stock are expected to be much more similar to those of the background stocks

than the marked chromosomes since it is more difficult to incorporate foreign genetical material by recombination than by independent assortment (Bartlett and Haldane, 1935). After synthesis, sc cv v f (A) and sc cv v f (D) females were respectively crossed to A and D males. From each of their F_2 generations, sc cv v f, sc cv + +, + + v f, and + + + + segregating males were isolated and mated to their sc cv v f sisters thus initiating four sublines (sc cv v f, sc cv + +, + + v f, and + + + +)for each background. These sublines were maintained through subsequent generations by mating their female 'representatives' (for example, + + v f females from the + + v f subline), to sc cv v f males every second generation. In the intermediate generations, the male 'representatives' were mated to sc cv v f females. The nature of sex-linked inheritance dictated the usage of this procedure with the result that recombination is expected to occur every second generation but not in the intermediate ones since there is virtually no crossing over in the male. The effects of recombination on egg production might be considerable depending on the distribution of 'egg production genes' on the X-chromosome. Females from the stocks, al dp b pr (A) and al dp b pr (D) were also crossed to A and D males, respectively and their F_1 female offspring backcrossed to al dp b pr males of the appropriate background. From each of their progeny, al dp b pr, al dp + +, + + b pr and + + + + males were isolated and each mated to their al dp b pr sisters thus initiating four sublines (al dp b pr, al dp + +, + + b pr, and + + + +) for each background. These sublines were maintained through subsequent generations by mating every generation, their male 'representatives' to al dp b pr females of appropriate background. Since there is practically no crossing over in the male, the effects of recombination in these experiments is expected to be negligible.

By examining appropriate differences between the egg production of these sublines, the effects of the segments, sc cv,v f, al dp and b pr were estimated

for each background. For example, the differences, + + v f - sc cv v f and + + + + - sc cv + +, provide estimates of the effect of the sc cv region. In addition, the difference between these differences estimates the interaction between the regions, sc cv and v f. Each of the four experiments (two chromosomes each on two backgrounds) was repeated twice by extracting each kind of female at two different points in the maintenance of the sublines.

All egg production was determined in the same manner: Males and females, a day or less in age, were set up, one pair per vial (23 x 85 mm) containing 10 ml of standard propionic acid medium (water, 1000 ml; agar, 19 g; sucrose, 54 g; brewer's yeast, 32 g; and propionic acid, 5 ml) and a spot of live yeast suspension on the surface. The vials were placed in a B.O.D. incubator at 25 C ± 1 C for three days. On the third day, each pair of flies was transferred to another vial containing fresh medium. On the fourth, fifth and sixth days, transfers were repeated (except that on the last day, all the flies were killed) and the eggs laid during each 24-hour interval were counted and the number recorded. Egg production was expressed as the number of eggs laid per female per day. The fourth to the sixth day of adult life is considered to be a sufficient length of time for egg production studies (Gowen, 1952). Females laying less than ten eggs were considered sterile (Buzzati-Traverso, 1955) and were omitted from the analysis.

Results

The egg production of the four segregating classes, sc cv v f, sc cv + +, + + v f and + + + + are recorded for each repeat and background in Table I. On the A background, sc^+ cv^+ flies laid on the average, about 23 eggs more than sc cv flies and an analysis of variance (Table II) showed that this difference is highly significant; the v f and sc cv x v f components were not significant.

On the D background, there was a highly significant interaction between repeats and 'treatments' (Table II). Nevertheless, $sc^+ cv^+$ females laid a consistently greater number of eggs than sc cv females, the differences (± their standard errors) being 27.6 ± 2.6 for the first repeat and 9.9 ± 3.2 for the second repeat. The v f component was not significant in the first repeat (mean effect, 5.2 ± 5.7) but was highly significant in the second repeat (mean effect, 19.8 ± 3.2). The sc cv x v f interaction was not significant in either repeat.

The egg production of the four segregating classes, al dp b pr, al dp + +, + + b pr, and + + + + are listed for each background and repeat in Table I. On both backgrounds, there were large al dp x b pr interactions (Table II) so that only simple effects were tested (Table III). On the A background, al^+ dp^+ flies lay about 26 eggs more than al dp flies if both are b pr; otherwise the difference is 37 eggs. The b pr segment exerts an effect only if all flies are al^+ dp^+, the mean difference being about 15 eggs. Similar statements for the D background can be made by examining Table III. In the fourth column of the table, a comparison of the second chromosomes of the A and D backgrounds is made. The difference, 'A - D' is positive (about 16 to 22 eggs) with respect to the al dp region but it is negative (about 11 to 16 eggs) with respect to the b pr region.

A detailed investigation of the sc cv region

The sc cv region was divided into two subregions, sc and cv and the correlation of egg production with each segment was studied. To accomplish this, sc cv v f (A) and sc cv v f (D) lines were extracted at the end of the twelfth cycle of backcrossing and crosses made to produce the sublines, sc cv v f, sc + v f, + cv v f, and + + v f. These sublines (hitherto written without v f) were maintained in the same manner as described for the earlier experiments involving sex-linked genes. The number of eggs laid by the female

representatives of these sublines was determined four and three times for the A and D backgrounds, respectively.

The fecundities of the four segregating classes are listed for each background and repeat in Table IV. Since an analysis of variance of the results (Table V) reveals that the triple interaction, sc x cv x repeats, for the A background is highly significant, a detailed analysis of individual comparisons for each repeat is presented in Table VI. For three of the four repeats, there were significant sc x cv interactions and of the four simple effects, 'cv in sc^+' (that is, $sc^+cv^+ - sc^+cv$) was consistantly significant at the 0.01 level of significance varying in magnitude from about 10 eggs to about 25 eggs. The main effect, cv, in repeat 2 is included since it estimates the same simple effect. Other patterns in individual comparisons were not evident. On the D background, the two-factor interaction, sc x repeats is highly significant. However, the magnitudes of the sc effect in repeats 1,2, and 3 were respectively, 5.7 ($p < .05$), -3.2, and -3.7 eggs, none of which are as large as the average cv effect of 12.4 ($p < .01$) eggs.

A prediction experiment

The above study seems to indicate that the cv segment, at least when in combination with the sc^+ region on the A background, exerts a considerable effect on egg production. If the cv segment is combined with another marked segment, it would be interesting to compare the joint effect of both segments in combination with a predicted value obtained from summing their individual effects.

A pure breeding cv (A) line was created by isolating a cv male from the F_2 of the P_1 cross: sc cv v f (A) ♀♀ x A ♂♂ and mating it with an A female. The cv (A) line was obtained from the F_3 generation of this latter

cross. The egg production of cv (A) females for two successive generations were 37.4 ± 1.8 (32 females) and 38.4 ± 1.9 (30 females). In our laboratory, I. McMillan had been repeatedly backcrossing in alternate generations, dp female segregants to A males. At the end of the ninth cycle, a dp (A) line was extracted and the mean egg production of 31 females was 41.1 ± 1.3.

The separate effects of cv and dp were estimated by measuring the egg production of all the F_2 segregants of the P_1 crosses: cv (A) ♀ x A ♂ and dp (A) ♀ x A ♂ (Table VII 'In separation' column). For the last cross, the F_2 phenotypically wild females were progeny-tested to determine their genotypes. The effects associated with the segments, cv and dp, estimated by the differences cv/± - cv/cv and dp/± - dp/dp, were 8.2 ± 2.5 and 10.9 ± 1.9 eggs, respectively. Thus, if cv and dp are additive for egg production, then cv/± dp/± females should exceed cv/cv dp/dp females by about 10.9 + 8.2 or 19.1 eggs. To test this hypothesis, cv females were mated with dp males and the number of eggs laid by the six kinds of females in the F_2 were measured (Table VII 'In combination' column). Again, the normal winged females were progeny-tested to determine their genotypes. The observed difference between cv/± dp/± and cv/cv dp/dp flies was 14.9 ± 2.4 which when tested against the expected difference of 19.1, is not statistically different (mean difference, 4.2 ± 3.9). Therefore, it would appear that the segments, cv and dp, are additive for egg production. This conclusion is arrived at perhaps less dramatically by an analysis of variance of the 'In combination' column of Table VII (Table VIII) in which it is shown that the cv x dp interaction component is not significant. The cv and dp components, as expected, are highly significant.

Discussion

These data illustrate that the inheritance of egg production is influenced by intrachromosomal effects and interactions as well as by the genetic background and perhaps, recombination. The results also provide in relation to the strains studied, some insight into the distribution and magnitude of effects of the genes or blocks of genes which in some way influence the trait.

Regional effects were clearly demonstrated in these experiments since females from the various sublines laid different numbers of eggs. However, in most cases, simple effects were computed due to the presence of two and three factor interactions. Intrachromosomal interactions were consistently absent in the X-chromosome on the D background and although there was no detectable interaction between the sc cv and v f regions on the A background, there was evidence for interaction within the sc cv segment. Interactions between the al dp and b pr regions of the second chromosome were large on both A and D backgrounds (11 and 16 eggs, respectively). Gilbert (1961) also detected some interactions within the second chromosome but these interactions could not be resolved into their separate components because the data were incomplete. The presence of heterogeneity in most of the experiments involving the X-chromosome is interpreted as a reflection of intra-subline genetic variation caused by recombination. Since the various X-chromosomal sublines were maintained every second generation by passage through their female 'representatives', recombination was allowed to occur. For example, a sc cv^+ female could have carried along with her markers a random assortment of 'egg production genes' whose origins were partly from the A (or D) X-chromosome and partly from the X-chromosome of the original sc cv v f (A) (or D) line, the relative proportions being dependent on the distribution of 'egg production genes' with respect to the markers. If linkage with the markers is tight and/or the marker genes pleiotropic for fecundity, heterogeneity of the magnitudes observed would not be expected to occur unless, perhaps, there

is a genuine interaction between the marker effects and repeats. This latter possibility is unlikely since a great deal of effort was expended in keeping the environment of the organisms constant from repeat to repeat. Also, if it is reasonable to argue from one set of markers to another regarding multiple marker effects, then the absence of 'treatment' x repeats interaction in the al dp b pr experiments in which recombination was essentially prevented would tend to support the premise that the heterogeneity in the sc cv v f experiments was due to recombination. Although the pleiotropic effects of the markers are totally confounded with the effects of their covered segments, the presence of heterogeneity, if interpreted as a reflection of the manifestations of recombination, can provide some insight into the distribution of the non-marker 'egg production genes' on the X-chromosome. Thus, the large sc cv effect, the almost negligible v f effect and the absence of heterogeneity in the sc cv v f (A) experiment suggests that the genes differentiating the X-chromosomes of the sc cv v f (A) and A strains are more concentrated within the sc cv segment. Consequently, one would expect interaction between 'treatments' and repeats to exist in the sc cv (A) experiment and indeed there was evidence for such interaction. On the D background, it is likely that the genes differentiating the first chromosomes of the D and sc cv v f (D) strains are more concentrated to the right of the sc cv region since there was heterogeneity in the sc cv v f (D) experiment.

The genetical difference between the A and D backgrounds with respect to the X-chromosome is qualitatively demonstrated by the respective presence and absence of heterogeneity in the sc cv v f (D) and sc cv v f (A) experiments as well as the respective presence and absence of sc x cv interaction in the sc cv (A) and sc cv (D) experiments. A numerical comparison of the second chromosomes of the A and D backgrounds was possible and it was revealed that the difference between their egg production with respect to the al dp segment

was positive (about 16 to 22 eggs) but negative (11 to 16 eggs) with respect to the b pr segment. These observations are of particular interest since it has been shown that at the time of these experiments, the females from the A and D strains lay approximately the same number of eggs (McMillan, 1967). That is, although the A and D strains are phenotypically the same with respect to egg production, this experiment clearly demonstrates their genotypic dissimilarity. If the markers on the second chromosome are pleiotropic for fecundity, their effects are obviated by making this 'A-D' computation to an extent which depends on the size of the interaction, if existent, between the markers and the rest of the chromosome.

The method of following the segregation of a metric trait with chromosomal markers has a number of drawbacks. Recall that the segregating genotypes whose fecundities are being compared are either homozygous recessive or heterozygous for their markers. If a dominant 'egg production gene', Ep, say (the egg production of Ep/Ep and Ep/ep are assumed to be the same), is linked with a recessive marker, a, then in a backcross of Ep a/ep A females to Ep a males, the difference between the egg production of A and a females would be zero since all the offspring would be either Ep/Ep or Ep/ep. Thus, dominant 'egg production genes' are not detectable by the method used here. Estimations of marker effects, non-marker effects and their interaction cannot be made separately although the comparison of backgrounds has provided a crude estimation of some non-marker effects. The information that certain markers are indeed pleiotropic for fecundity as well as knowledge of the magnitude of their effects would make them a valuable tool in studying the phenogenetics of egg production. Similarily, identification and location of non-marker 'egg production genes' and consequently, a study of their physiological and biochemical functions would provide a solid basis for the investigation of the genetics of a fitness trait. Identification, location, and study of the function of polygenes

controlling traits like the production of crossveins (Milkman, 1960; Mohler, 1967) and the number of sternopleural chaeta (Thoday, 1961; Spickett and Thoday, 1966) have been achieved with a certain amount of success. Although the experiments reported in this paper are not as sophisticated as those of the above authors, the results provide a basis for performing more critical and definitive investigations into a trait which is perhaps of greater significance from an applied and evolutionary standpoint than crossveins and sternopleural chaeta number.

The segments, cv and dp were placed in combination and their joint effect was approximately equal to an estimate based on the sum of their individual effects. This experiment had no great underlying aim but was simply designed to show that despite the fact that the inheritance of egg production is probably a complex phenomenon and subject to large variation, a certain degree of success in making predictions can be achieved.

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TABLE I

Segregation of egg production with four segments of the first and second chromosomes

Chromosome I	Background A		Background D	
Genotype	Repeat 1	Repeat 2	Repeat 1	Repeat 2
sc cv v f	37.1 (27)	36.5 (7)	39.3 (24)	45.3 (20)
sc cv + +	36.6 (15)	41.8 (4)	46.8 (30)	64.4 (20)
+ + v f	61.2 (36)	60.0 (23)	69.6 (36)	57.5 (20)
+ + + +	60.4 (35)	55.2 (14)	72.3 (31)	75.0 (20)

Chromosome II	Background A		Background D	
Genotype	Repeat 1	Repeat 2	Repeat 1	Repeat 2
al dp b pr	31.2 (25)	23.8 (16)	24.8 (17)	27.3 (22)
al dp + +	35.5 (19)	28.5 (10)	38.0 (14)	43.8 (29)
+ + b pr	56.3 (35)	50.3 (18)	22.6 (8)	33.9 (21)
+ + + +	69.6 (38)	69.4 (24)	58.8 (14)	63.5 (18)

(·) -- number of females

TABLE II

Analysis of variance of egg production results

Chromosome I	Background A			Background D		
Source	d.f.	MS	F	d.f.	MS	F
sc cv	1	18,012	93.3**	1	21,425	106.1**
v f	1	31	NS	1	5,843	28.9**
sc cv x v f	1	1	NS	1	280	NS
repeats	1	63	NS	1	688	NS
repeats x 'treatments'	3	110	NS	3	2,163	10.7**
error	153	193		193	202	

Chromosome II	Background A			Background D		
Source	d.f.	MS	F	d.f.	MS	F
al dp x b pr	1	1,291	9.9**	1	2,466	19.0**
repeats	1	948	7.3**	1	1,107	8.5**
repeats x 'treatments'	3	133	NS	3	103	NS
error	177	130		135	130	

** $p < .01$, NS -- not significant

TABLE III

Analysis of individual effects of two regions of chromosome II

Effect	Background A	Background D	A-D
aldp in b pr	25.7**	4.2	21.5**
in b^+ pr^+	36.5**	20.2**	16.3**
b pr in al^+ dp	4.5	15.2**	-10.7**
in al^+dp^+	15.3**	31.7**	-16.4**

** $p < .05$

TABLE IV

Segregation of egg production with the genes, sc and cv

Background A (n = 27 in each cell)				
Genotype	Repeat 1	Repeat 2	Repeat 3	Repeat 4
sc cv	36.6	34.9	38.6	38.2
sc +	39.1	44.3	44.8	33.7
+ cv	35.2	29.8	37.6	27.1
+ +	51.7	39.9	54.2	52.0

Background D (n = 25 in each cell)			
Genotype	Repeat 1	Repeat 2	Repeat 3
sc cv	35.4	35.1	38.4
sc +	52.5	46.3	48.0
+ cv	42.9	32.0	32.4
+ +	55.2	43.0	46.6

TABLE V

Analysis of variance of egg production results for the *sc* and *cv* regions

	Background A			Background D		
	d.f.	MS	F	d.f.	MS	F
sc	1	507	4.4*	1	28	NS
cv	1	11,306	98.3**	1	11,819	98.2**
sc x *cv*	1	4,975	43.3**	1	1	NS
repeats	3	989	8.6**	2	1,427	11.9**
sc x repeats	3	325	NS	2	612	5.1**
cv x repeats	3	19	NS	2	92	NS
sc x *cv* x repeats	3	1,218	10.6**	2	134	NS
error	416	115		288	120	

* $p < .05$, ** $p < .01$, NS -- not significant

TABLE VI

Analysis of individual egg differences for the sc and cv regions on the A background

Contrast	Repeat 1	Repeat 2	Repeat 3	Repeat 4
sc in cv	-1.4	-4.7*	-1.0	-11.1**
in cv^+	12.6**		9.3**	18.3**
cv in sc	2.5	9.8**	6.3*	-4.4
in sc^+	16.5**		16.6**	24.9**
sc x cv	14.0**	0.7	10.3*	29.3**

* $p < .05$, ** $p < .01$

TABLE VII

Egg production of F_2 segregants
for the genes, cv and dp

In separation		In combination	
cv/cv	36.3 ± 2.0 (37)	cv/cv dp/dp	33.7 ± 1.8 (34)
cv/+	44.5 ± 1.4 (31)	cv/cv dp/+	42.4 ± 1.3 (48)
dp/dp	39.5 ± 1.7 (35)	cv/cv +/+	42.0 ± 1.7 (21)
dp/+	50.4 ± 1.1 (51)	cv/+ dp/dp	36.1 ± 1.8 (35)
+/+	49.3 ± 1.9 (23)	cv/+ dp/+	48.6 ± 1.5 (50)
		cv/+ +/+	46.6 ± 2.4 (19)

(·) -- number of females

TABLE VIII

Analysis of variance of results from the prediction experiment

	d.f.	MS	F
cv	1	1,107	11.7**
dp	2	2,457	25.9**
cv x dp	2	70	NS
error	201	95	

** $p < .01$, NS -- not significant