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Selection for high and low number of sternopleural bristles in *Drosophila ananassae*: Correlated response in the frequency of chromosome inversions

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Directional selection for high and low number of sternopleural bristles in ***Drosophila ananassae*** *was applied for 13 generations. The selection produced a rapid divergence in the mean number of sternopleural bristles in the replicates high and low lines: i- high (H_1 - 25.75, H_2 - 25.69); ii- low (L_1 - 14.16, L_2 - 13.55); iii- control (17.21) lines in G_{13}. Regression coefficients for the high and low lines were significantly different from zero. The realized heritability over thirteen generations was 21-23 for the high lines and 14-18 for the low lines. The results suggest that the number of sternopleural bristles in* ***D. ananassae*** *is under polygenic control, with a substantial amount of additive genetic variation.*

Flies of the base population had three chromosome inversions: AL (2L), ZE (2R) and DE (3L). The comparison of chromosome arrangement between high and low lines (the G_{13} generation of selection) indicates significant changes in the inversion frequency during the course of selection, providing evidence for correlation between the bristle number and particular chromosome arrangements.

Key words*: directional selection,* ***Drosophila ananassae****, inversion frequencies, sterno-pleural bristle number.*

INTRODUCTION

Knowledge of the genetic basis of phenotypic changes is essential for understanding how operates evolution in Mendelian populations (Lande, 1983). Many morphological features of organisms are quantitative in nature. It is important to clarify the genetics of quantitative variation in morphological traits. Polygenes with a small effect on a particular character may supplement each other to produce observable quantitative differences; the effects of polygenes are considered additive. Environmental effects may also produce deviations from the expected phenotypes. Quantitative characters may also be controlled by few major genes supplemented by numerous genes with small effects (Shrimpton and Robertson, 1988b).

The genetics of quantitative traits has been extensively studied in *Drosophila melanogaster* by using different bristle phenotypes, particularly sternopleural and abdominal bristle number (Breese and Mather, 1957; Barnes, 1968; Parsons, 1970; López-Fanjul and Hill, 1973; Schnee and Thompson, 1984; Shereif and Skibinski, 1988a,b; Shrimpton and Robertson, 1988a,b; Mackay *et al*, 1994). Sternopleural bristle phenotypes in *D. melanogaster* have been frequently employed to study the effect of artificial and natural selection and to throw light on the genetic constitution of natural populations (Parsons, 1970; Gibson and Thoday, 1963,

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1964; Barnes, 1968; López-Fanjul and Hill, 1973; Kearsey and Barnes, 1970; Schnee and Thompson, 1984; Shereif and Skibinski, 1988a; Capy *et al,* 1993; Mackay *et al,* 1994). Effects of different chromosomes on sternopleural bristle number have been detected and different genetic factors controlling sternopleural bristle number have been located in different chromosomes by using marker strains (Breese and Mather, 1957; Thoday, 1967, 1973; Lopez-Fanjul and Hill, 1973; Thoday and Thompson, 1976; Shrimpton and Robertson, 1988a,b). Genetic heterogeneity for sternopleural bristle number has been found in Indian populations of *D. melanogaster* (Singh and Mathew, 1993). Intermediate phenotypes for sternopleural bristle number were significantly more heterozygous at certain allozyme loci than more extreme ones, which supports additive and homeostatic models for gene action and this could explain the higher heterozygosity of central phenotypes (Shereif and Skibinski, 1988b). In certain cases, association between chromosomal inversion polymorphism and morphometric characters has been reported (Prevosti, 1967; Aguade and Serra, 1980; Martinez-Sebastian and de Frutos, 1986; Garcia-Vazquez *et al,* 1989; Singh and Das 1991).

Drosophila ananassae is a cosmopolitan and domestic species. It belongs to the *melanogaster* species group of the subgenus *Sophophora*. This species occupies a unique status in the whole of genus *Drosophila* due to certain peculiarities in its genetical behaviour (Singh, 1985). A number of investigations on genetics of *D. ananassae* – particularly population genetics, crossing-over, behaviour genetics and mutagenesis– have been carried out by numerous investigators (for references see Singh, 1985, 1996; Tobari, 1993). Population genetics of three cosmopolitan inversions in Indian *D. ananassae* has been extensively studied and the results obtained provide evidence for genetic differentiation in its natural populations (Singh, 1989). Genetic heterogeneity for metrical characters –such as sternopleural bristle number and sex-comb teeth number– has also been found in Indian populations of *D. ananassae* (Singh and Lata, 1994; Singh and Mathew, 1995). Mean sternopleural bristle number in *D. ananassae* is lower than *D. melanogaster*, and females possess more bristles than males (Singh and Mathew, 1995).

On the basis of positive response to selection, evidence for polygenic control and additive genetic variation has been presented for phototactic behaviour, mating propensity, spontaneous male recombination and pupation height (Markow and Smith, 1979; Singh and Chatterjee, 1988; Mohanty and Singh, 1992; Singh and Pandey, 1993). Thus *D. ananassae* is characterised by a considerable degree of additive genetic variation with respect to a variety of traits. However, the effect of selection on morphometric character such as sternopleural bristle phenotypes –which has been extensively studied in *D. melanogaster*– has not been investigated in *D. ananassae*. In view of this, we studied the effect of directional selection of sternopleural bristle phenotypes in *D. ananassae* and we also studied inversion polymorphism in the base population, selection and control lines to test the relationship between chromosome arrangements and bristle number.

MATERIALS AND METHODS

In order to test the effect of directional selection on the number of sternopleural bristles in *D. ananassae*, a base population was constructed by crossing five mass culture stocks of different geographic origins (Jammu, Varanasi, Baripada, Madras and Kanniyakumari). Virgin females and males of each stock were reciprocally crossed and the hybrids were randomly used to originate the base population. It was maintained for five generations of random mating. After 5th generation, bidirectional selection was applied for high and low number of sternopleural bristles. From the base population, virgin aged 3-4 days females and males were collected at random and the number of bristles (on left and right body sides) in 100 females and 100 males was counted. The mean number of sternopleural bristles per fly was calculated by combining the data of females and males, which is the mean number of G_0 generation. From these flies,

Table I

Variation of mean number (± SEM) of sternopleural bristles in *Drosophila ananassae* during thirteen generations of selection to high (H) and low (L) number. Selected lines were replicated. (Data of control line also given).

Generation of selection	High line		Low line		Control population
	H_1	H_2	L_1	L_2	C
Base population					17.17±0.097
1	18.87±0.152	18.73±0.136	17.73±0.132	17.42±0.125	17.51±0.143
2	18.43±0.375	18.39±0.146	16.61±0.134	16.48±0.124	16.95±0.136
3	19.16±0.175	18.50±0.176	15.91±0.145	16.32±0.127	17.59±0.158
4	19.76±0.188	19.07±0.177	16.44±0.162	15.71±0.107	17.66±0.138
5	22.26±0.245	21.46±0.419	16.29±0.168	15.97±0.169	18.08±0.155
6	22.66±0.316	23.30±0.244	16.61±0.159	15.60±0.130	19.07±0.187
7	21.81±0.221	22.22±0.104	15.51±0.143	14.56±0.126	18.03±0.149
8	24.00±0.249	24.48±0.290	15.09±0.125	14.44±0.105	17.85±0.127
9	23.79±0.313	23.14±0.251	14.72±0.130	14.18±0.118	17.20±0.129
10	23.88±0.268	23.46±0.198	14.25±0.106	13.88±0.123	17.17±0.142
11	25.49±0.120	25.26±0.271	14.19±0.113	13.61±0.105	17.37±0.299
12	25.89±0.297	25.69±0.263	14.42±0.119	13.68±0.112	18.47±0.188
13	25.75±0.280	25.69±0.326	14.16±0.104	13.55±0.102	17.21±0.180

two replicates of high line (H_1, H_2) and two replicates of low line (L_1, L_2) were set up. A control line was initiated by taking at random a sample of 10 flies of each sex from the base population. Two groups each of 10 females and 10 males with highest bristle number were crossed to start the high (H_1, H_2) lines. Another two groups of 10 females and 10 males showing lowest bristle number were also crossed to initiate the low (L_1, L_2) lines. In control line, bristle number of 50 females and 50 males was counted in each generation and a random sample of 10 females and 10 males was transferred to get next generation. In the selected lines, virgin females and males were collected and the bristle number was scored in 50 females and 50 males in each of the four lines. In high line, 10 females and 10 males with highest bristle number were transferred to a culture bottle to obtain next generation. In low line, 10 females and 10 males with lowest bristle number were transferred to a culture bottle to originate the next generation. This was repeated in every generation of selection experiment. The selection experiment was continued for 13 generations. All the cultures were maintained in the laboratory under standard conditions (temperature approximately 24°C) on the normal agar-yeast culture medium. After G_{13}, the high and low lines were reciprocally crossed and the bristle number of 50 hybrids of each sex and cross was recorded.

In order to test the relationship between bristle number and chromosome arrangement

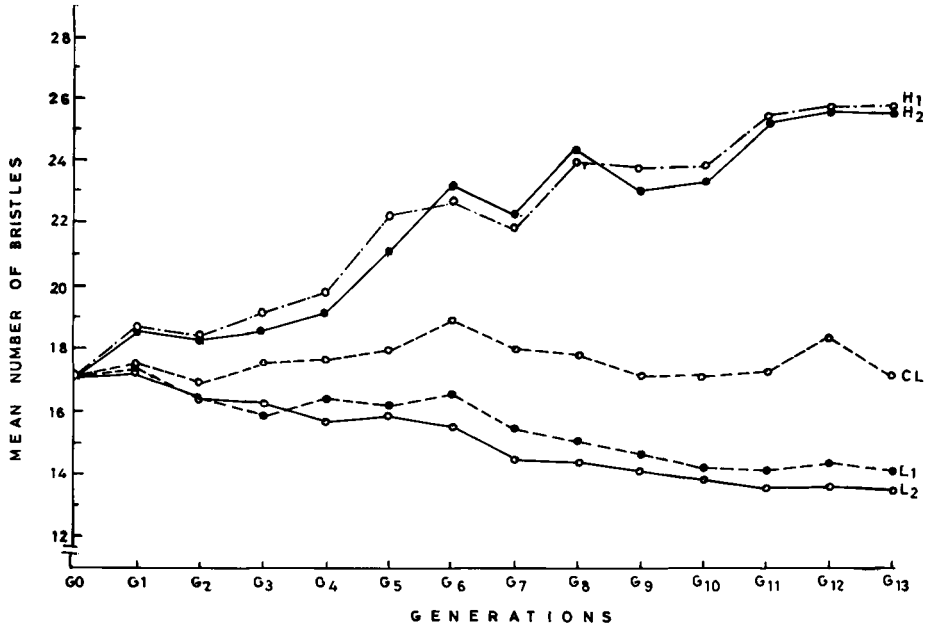

Fig 1. Mean number of sternopleural bristles in selection experiment in high (H_1, H_2), low (L_1, L_2) and control (C) lines in *Drosophila ananassae*.

frequency, chromosomal analysis of base population was done before starting the selection experiment. Chromosomal analysis was again made after G_{13} generation of selection of all the five lines (H_1, H_2, L_1, L_2 lines and the control C population). Chromosomal analysis of base population was performed by squashing 100 third instar larvae. After G_{13}, chromosomal analysis of all the five lines was done by squashing larvae (52-L_1, 55-L_2, 50-H_1, 5_1-H_2 and 60-control). Usual lacto-aceto-orcein method was used (Singh *et al,* 1995).

RESULTS

Table I and Figure 1 show the mean number of sternopleural bristles in flies selected during 13 generations for high and low bristle number. The control line is also shown. Mean number of sternopleural bristles per fly is 25.75 and 25.69 in two replicates of high line, 14.16 and 13.55 in two replicates of low line and 17.21 in control line. From Figure 1, it is apparent that the response to selection for high bristle number was rapid from early generation of selection and selection response was slower in low lines. Table II shows realized heritability, regression coefficient (regression of generation mean on generation number) and results of test of significance for H_1, H_2, L_1 and L_2 lines. Realized heritabilities over 13 generations of selection were 0.214 (H_1), 0.231 (H_2), 0.139 (L_1) and 0.183 (L_2). Regression coefficients are 0.709 (H_1), 0.713 (H_2), 0.929 (L_1) and 0.959 (L_2). Results of test of significance show significant deviation from zero slope for all four lines ($P < 0.001$).

In the 13th generation of selection, high and low lines were reciprocally crossed to produce F_1 hybrids. Bristle number of hybrids was scored. Mean number of bristle in selection lines at G_{13} and in crosses (F_1) is presented in Table III. Mean number of bristles in hybrids ranges from 17.19 to 19.27 in different crosses, which shows that hybrids possess intermediate bristle number between high and low lines.

Chromosomal analysis of base population before starting the selection experiment, and of H_1, H_2, L_1, L_2 and control lines after G_{13} was made and different inversions in the second and third chromosomes were detected. Total number of chromosomes examined, frequencies of different gene

Table II

Realized heritability (h^2), regression coefficient (b) and results of test of significance for H_1, H_2, L_1 and L_2 lines

Line	$h^2 \pm$ SE	b	*df*	*t*	P <
H_1	0.214 ± 0.008	0.709 ± 0.022	11	8.885	0.001 *
H_2	0.231 ± 0.007	0.713 ± 0.029	11	6.790	0.001 *
L_1	0.139 ± 0.016	0.929 ± 0.041	11	6.235	0.001 *
L_2	0.183 ± 0.011	0.959 ± 0.027	11	9.989	0.001 *

* Significance.

Table III

Mean number of sternopleural bristles (M) in selection lines at generation 13 and in crosses between them. (Sample size = 50 females and 50 males).

Line	Female	Male	M ± SEM
Selected:			
L_1	L_1	L_1	14.16 ± 0.104
L_2	L_2	L_2	13.55 ± 0.102
H_1	H_1	H_1	25.75 ± 0.280
H_2	H_2	H_2	25.69 ± 0.326
F_1 Hybrids:			
$L_1 \times H_1$	L_1	H_1	17.19 ± 0.149
$H_1 \times L_1$	H_1	L_1	19.27 ± 0.184
$L_1 \times H_2$	L_1	H_2	17.51 ± 0.215
$H_2 \times L_1$	H_2	L_1	18.37 ± 0.165
$L_2 \times H_1$	L_2	H_1	17.26 ± 0.167
$H_1 \times L_2$	H_1	L_2	17.96 ± 0.171
$L_2 \times H_2$	L_2	H_2	17.20 ± 0.182
$H_2 \times L_2$	H_2	L_2	17.31 ± 0.141

Table IV

Frequency (in percentage) of ST and inverted gene orders in 2L, 2R and 3L in the base population (G_0) before starting the experiment, and in H_1, H_2, L_1, L_2 and control lines after G_{13}

Line	N	2L		2R		3L		M
		ST	AL	ST	ZE	ST	DE	
Base population	200	55.50	44.50	81.50	18.50	86.50	13.50	1.23
Control	120	64.17	35.83	68.33	31.67	100.00	0	1.35
H_1	100	64.00	36.00	64.00	36.00	100.00	0	1.44
H_2	102	65.69	34.31	65.69	34.31	100.00	0	1.37
L_1	104	38.46	61.54	100.00	0	76.92	23.08	0.85
L_2	110	42.73	57.27	100.00	0	91.82	8.18	0.65

N = Number of chromosomes examined.
M = Mean number of heterozygous inversions per individual.

arrangements and level of inversion heterozygosity in base population and different lines are given in Table IV. The chromosomal analysis revealed the presence of three inversions : AL(2L), ZE(2R) and DE (3L). The location of these inversions in different chromosomes of *D. ananassae* is depicted in Figure 2. The data on inversion frequencies in the base population have been analysed to test Hardy-Weinberg proportions and intra- and interchromosomal interactions and the results have been described elsewhere (Singh *et al,* 1995). Out of these three inversions, two (AL and DE) are cosmopolitan inversions and the third one, *i.e.*, ZE was detected for the first time in a laboratory stock established from a female collected from Madurai in December 1984 (Singh and Singh, 1991). These inversions have been found to persist in laboratory stocks (Singh, 1982; Singh and Singh, 1991). In the base population, all the three inversions were present at substantial frequency before starting the experiment and AL inversion was more frequent than the other two inversions. In two replicates of high line, DE (3L) inversion was eliminated during the course of selection and the lines became monomorphic for ST gene order in the third chromosome. In both replicates of high line, the frequency of ZE inversion has increased and the frequency of AL inversion has decreased as compared to the base population. The level of inversion heterozygosity has also increased in both the replicates of high line in comparison with the base population. When the comparison of chromosomal variability is made between the base population and low line, there is a considerable change in the chromosomal constitution of low line during the course of selection. These changes are: *i*- decrease in the level of inversion heterozygosity; *ii*- in both replicates of low line DE inversion was retained during the course of selection but ZE was eliminated, and 2R became monomorphic for ST gene order; *iii*- AL chromosomes were more frequent in both

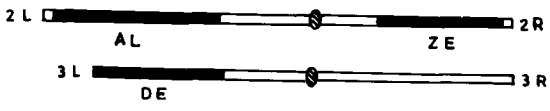

Fig 2. Location of AL, ZE and DE inversions in different chromosomes of *Drosophila ananassae.*

replicates of low line than the base population. Thus, there were significant changes in the degree of chromosomal variability and in the frequencies of chromosome arrangements in high and low lines. The chromosomal analysis of the control line after G_{13} revealed that DE was lost and the frequency of AL, ZE and the level of inversion heterozygosity were similar to those in high line.

DISCUSSION

It is evident from the results that selection for high and low number of sternopleural bristles in *D. ananassae* was effective. As a consequence, two lines which differ in the mean number of bristles were obtained. The mean number of bristles in the control line remained very close to that of the base population. Thus in *D. ananassae*, the nature of response to selection for sternopleural bristles indicates additive genetic variation for this trait. The intermediate bristle number in F_1 hybrids obtained by crossing high and low lines suggests a polygenic control for the trait. Furthermore, an asymmetric response to selection was also obtained. That is the selection applied was more rapid in the high lines than in the low lines.

The asymmetrical response to artificial selection has been reported earlier in several studies which results from genetic asymmetry (Frankham, 1990). In the case of *D. melanogaster*, it is believed that the increased variance in the high lines compared to that in low lines is due to accumulation of new mutations on the loci controlling bristle number (Mackay *et al*, 1994). Non-linearity would be expected in the phenomenon of accelerated response to selection (Mather and Harrison, 1949), since this is due to the occurrence of recombinants for high chaeta number between interacting polygenes. The recombinants are then favoured by selection, and so chaeta number would rise rapidly.

Chromosomal analysis of the base population revealed that it was polymorphic for three inversions: AL(2L), ZE(2R) and DE (3L). These inversions cover considerable length of the second and third chromosomes (see Fig 2). In the H_1, H_2, L_1, L_2 and control lines, it was found that significant changes had occurred in the selection lines with respect to chromosome arrangement frequencies during the course of selection. Both the replicates of high line were fixed for ST gene arrangement in the third chromosome due to the loss of DE inversion. However, both replicates of low line remained polymorphic in the third chromosome due to the persistence of DE inversion. Similarly, there were significant differences between the high and low lines with respect to the frequencies of gene orders in the second chromosome. Both L_1 and L_2 were fixed for ST gene order in 2R due to loss of ZE inversion but H_1 and H_2 remained polymorphic in 2R due to persistence of ZE inversion at considerable frequency. The 2L remained polymorphic in both high and low lines, but the frequency of AL inversion was higher in both replicates of low line as compared to high line. Furthermore, the level of inversion heterozygosity was more pronounced in the high line than in the low line. Thus, the lines for high and low number of sternopleural bristles had undergone considerable changes with respect to chromosomal variability during the course of selection and selection lines showed significant changes from the base population. However, the control line remained similar to the high line after G_{13}.

Comparison of chromosome arrangement frequency between high and low lines indicates that there is a correlation between the bristle number and chromosome arrangement frequency in *D. ananassae*. High mean number of bristles is correlated with ST (2L), ZE (2R) and ST (3L) arrangements, and low number of bristles correlates with AL (2L), ST (2R) and DE (3L). Thus, these findings provide evidence that a significant gene activity affecting bristle number is present in both major autosomes (II and III) of *D. ananassae*.

The present study in *D. ananassae* is the first report of correlation between the number of sternopleural bristles and chromosome arrangement frequency. There are few studies concerning the relation between inversion polymorphism and morphometric variation. A significant correlation between

chromosome arrangements and body size has been observed in *Moraba scurra* (White and Andrew, 1960). Butlin *et al* (1982) reported a correlation between wing length in males and three different karyotypes of chromosome I in *Coelopa frigida*. Prevosti (1967) investigated the relationship between wing length and inversion polymorphism in *D. subobscura*. Selection for long wings favours heterozygous combination for ST with inversions. However, selection for short wings generally fixes in homozygous combination specific complex inversion order. Prevosti (1967) suggested that genes for short wings are located in inverted gene orders, but genes for long wings lie in ST gene order which occurs in heterozygous combination with inversions. A significant association between inversion polymorphism and wing lengths and between inversions and extra scutellar and dorsocentral bristles in *D. melanogaster* has also been reported (Aguade and Serra, 1980; García-Vázquez *et al*, 1989; Singh and Das 1991). Selection for increased phenotypes of extra bristles corresponded with identical pattern of response in the frequency of In (3R) C inversion in *D. melanogaster* (Das and Singh, 1992). While selecting for abdominal bristle number in *D. subobscura*, Martinez-Sebastian & de Frutos (1986) found that structural homozygosity was generated in both directions of selection. In some chromosomes, the same gene arrangement was fixed in the high selection lines but not in the low selection lines, but in other chromosomes the reverse was true (Martinez-Sebastian and de Frutos, 1986). The role of O chromosome of *D. subobscura* on the manifestation of abdominal bristle number was analyzed in detail by performing bidirectional selection experiments by García-Augustín *et al* (1993). They suggested that chromosome 3R of *D. melanogaster* and chromosome O of *D. subobscura* retain similar function as it has been found that the third chromosome of *D. melanogaster* influences abdominal bristle number (Davies, 1971). The present results indicate that both major autosomes (II and III) influence sternopleural bristle number as there are significant changes in the frequency of gene arrangements in both the chromosomes of *D. ananassae*.

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