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Population Genetics of *Drosophila ananassae*: Variation in the Degree of Genetic Divergence in Populations Transferred to Laboratory Conditions

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Pranveer Singh and Bashisth N. Singh (2008) Population genetics of *Drosophila ananassae*: variation in the degree of genetic divergence in populations transferred to laboratory conditions. *Zoological Studies* **47**(6): 704-712. Forty-five laboratory populations of *Drosophila ananassae* initiated from females collected from different eco-geographical localities of India were maintained for several generations (a minimum of 10) and analyzed chromosomally to determine the frequencies of 3 cosmopolitan inversions. All laboratory populations under study showed variations with respect to the frequencies of the 3 cosmopolitan inversions, and remained polymorphic even after 10 generations, suggesting that heterotic buffering may be associated with the 3 cosmopolitan inversions in *D. ananassae*. Comparison of the same data with corresponding natural populations showed considerable changes in the frequencies of inversions and level of inversion heterozygosity between laboratory and natural populations. The degree of genetic divergence between initial and final populations of *D. ananassae* was quantified by calculating the genetic identity (I) and genetic distance (D) on the basis of differences in chromosome arrangement frequencies. Laboratory populations of *D. ananassae* showed variations in the degree of genetic divergence when transferred and maintained for several generations under laboratory conditions. Populations coming from similar environmental conditions and showing an initially high degree of genetic similarity had diverged to different degrees. Variations in the degree of genetic differentiation between different natural and laboratory populations are likely due to genetic drift.
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Key words: *Drosophila ananassae*, Laboratory populations, Chromosome inversions, Genetic divergence, Genetic drift.

In *Drosophila*, chromosomal polymorphism due to inversions is a common occurrence and is often maintained by balancing selection (Da Cunha 1960, Dobzhansky 1970, Sperlich 1973). Thus, chromosomal polymorphism is adaptively important in *Drosophila*. Each chromosomal arrangement possesses groups of genes organized by selective forces to produce an adaptive phenotype either by itself or in combination with other arrangements of the same chromosome. Thus, a well-adapted *Drosophila* population may respond to fluctuations in its environment by altering its net gene pool, either by changing the frequencies of chromosomal arrangements or by redistributing the genic contents of any chromosomal unit (Spiess 1957). However, patterns of chromosomal polymorphism vary in different species of *Drosophila* (Singh 2001). Geographically widespread species of *Drosophila* are expected to be chromosomally more polymorphic because they are ecologically more versatile (Da Cunha and Dobzhansky 1954).

In many species of *Drosophila*, inversions have been found to persist for a number of generations when populations are transferred to laboratory conditions. In *D. pseudoobscura*, inversions persisted in laboratory populations for many generations due to adaptive superiority of inversion heterozygotes (Levene and Dobzhansky 1958). Experiments were performed on different species of *Drosophila* to determine the genetic

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mechanisms of the maintenance of inversion polymorphisms when populations were transferred to a laboratory environment. In certain cases, inversions were found to decrease in frequency or were totally eliminated, e.g., *D. pseudoobscura* (Dobzhansky and Spassky 1962, Watanabe et al. 1970), *D. subobscura* (De Frutos 1978), *D. paulistorum* (Powell and Richmond 1974), and *D. melanogaster* (Inoue 1979, Singh and Das 1992). However, a low level of change was detected in certain other studies, e.g., *D. persimilis* (Spiess 1950), *D. subobscura* (Sperlich et al.1976, Krimbas and Loukas 1980), *D. robusta* (Carson 1961), and *D. ananassae* (Singh and Singh 2004). An increase in the degree of inversion polymorphism was found in *D. bipectinata* populations when transferred to laboratory conditions (Singh and Banerjee 1997).

Drosophila ananassae is a cosmopolitan and domestic species. It harbors a large number of inversions in its natural populations (Singh 1998). Most of these inversions have a restricted distribution, while the 3 cosmopolitan inversions, namely, alpha (AL) in 2L, delta (DE) in 3L, and eta (ET) in 3R, have worldwide distributions (Singh 1998). Population genetics of chromosomal polymorphisms in natural Indian populations of *D. ananassae* have been studied (for references see Singh 1998), and results have clearly shown that there is geographic differentiation of inversion polymorphisms in Indian populations. Furthermore, populations from South India are genetically more divergent when compared to those from North Indian populations. Thus, the cosmopolitan inversions in *D. ananassae* have been subjected to natural selection.

Chromosomal polymorphisms due to cosmopolitan inversions often persist in laboratory populations of *D. ananassae* established from females collected from nature (Singh 1982 1983a b 1987). Some populations maintained for hundreds of generations in a laboratory environment have been found to contain these inversions. This demonstrates that heterotic buffering is associated with these inversions. However, the degree of heterosis may vary depending on the allelic contents of the chromosome variants (Singh 1983b). Evidence for persistence of heterotic buffering associated with cosmopolitan inversions in interracial hybridization experiments has been presented, and involves chromosomally polymorphic and monomorphic strains of *D. ananassae* (Singh 1972 1974 1981 1985). Based on these findings, it was suggested that heterotic buffering associated with cosmopolitan inversions in *D. ananassae* appears to be simple luxuriance rather than population heterosis (coadaptation), and thus luxuriance can function when organisms adjust to their environments (Singh 1985).

The present communication reports data on the frequencies of the 3 cosmopolitan inversions in laboratory populations of *D. ananassae* and the degree of genetic divergence at the level of chromosomal polymorphism in *D. ananassae* populations when transferred to laboratory conditions. Forty-five natural populations of *D. ananassae* from different ecogeographic regions of India were analyzed for chromosome inversions. Data obtained on the frequency of inversions and level of inversion heterozygosity were reported elsewhere (Singh and Singh 2007). Mass culture stocks established from these collections were maintained in the laboratory for several generations for subsequent chromosomal analysis.

MATERIALS AND METHODS

Forty-five laboratory populations of *D. ananassae* were established from females collected from different localities in India (Fig. 1). Details of collections are given in table 1. All stocks were maintained on simple culture medium by transferring about 50 flies (with equal numbers of males and females) to fresh food bottles in each generation under normal laboratory conditions (24 ± 1°C). After several generations (a minimum of 10), chromosomes of these populations were analyzed by squashing 100 larvae taken randomly from each laboratory stock following the lacto-aceto-orcein method (see Strickberger 1962, Richardson and Yoon 1973), and data on frequencies of different gene arrangements and the level of inversion heterozygosity were obtained. To study the genetic divergence at the level of chromosomal polymorphisms when populations were transferred to laboratory conditions, the genetic identity (I) and genetic distance (D) between initial and final populations were calculated on the basis of differences in chromosome arrangement frequencies following the formula of Nei (1972).

RESULTS

Chromosomal analysis of laboratory populations of *D. ananassae* showed the presence of all

the 3 cosmopolitan inversions, although some of the laboratory populations became homozygous for standard or inverted gene arrangements. However, none of the populations became completely monomorphic. Frequencies (in percent) of inversions in different laboratory populations of *D. ananassae* are given in table 2. Frequencies of inversions in corresponding natural populations (Singh and Singh 2007) are given in parentheses in the same table. Out of 45 laboratory populations analyzed, 6 populations (BN, DN, AD, DW, GU, and PN) had become monomorphic in 2L for the AL inversion, while 8 populations (PU, LK, RP, UJ, JR, RJ, MA, and GU) had become monomorphic in 3L for the standard gene arrangement. Nine populations (BL, PA, CW, DN, HD, UJ, IN, MU, and NA) had become monomorphic in 3R for the standard gene arrangement.

When laboratory populations were compared with corresponding natural populations with respect to the frequencies of AL inversions, there was considerable change in some of the populations, with both increasing and decreasing trends observed, although most of the populations had maintained more or less similar frequencies. The same was true for the DE inversion in 3L and the eta inversion in 3R (Table 2). In general, the persistence of inversions continued to decrease from AL to ET, while the rate of loss followed the reverse order (see Table 2 for comparison). The level of inversion heterozygosity reflected through the mean number of heterozygous inversions per individual ranged from 0.148 in RP to 1.48 in PJ (Table 2). This shows that both increasing and decreasing trends differed little in most populations. The frequencies of the 3 cosmopolitan inversions

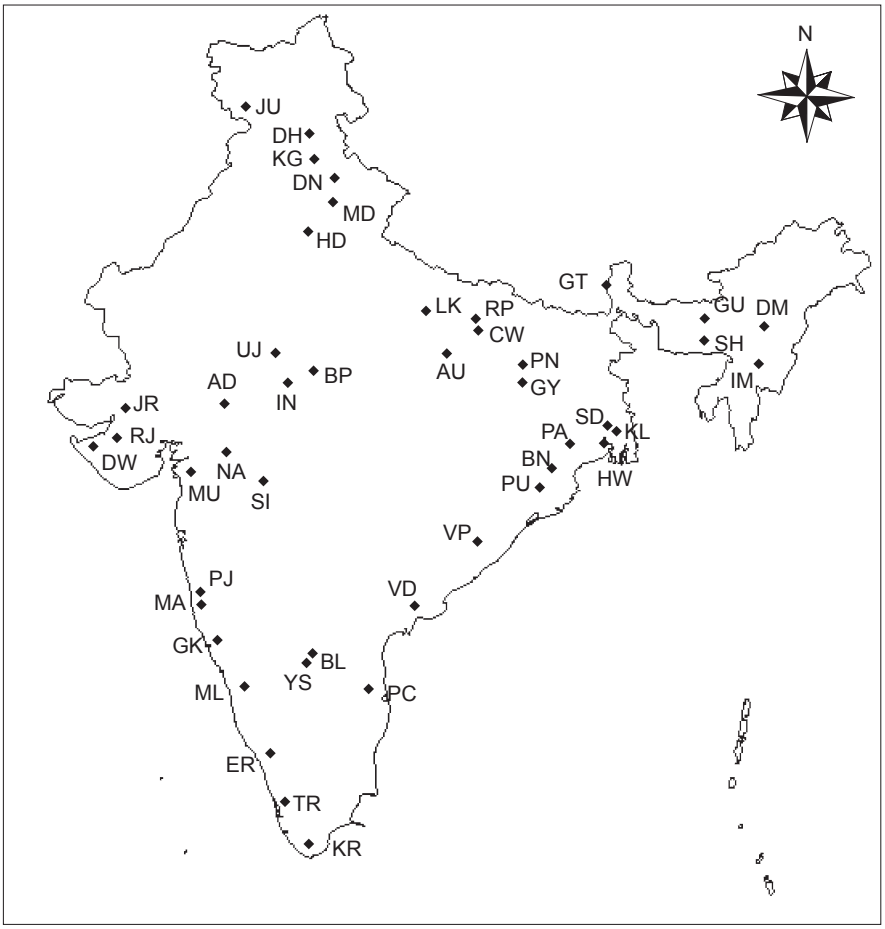

Fig. 1. Map of India showing the localities from where *Drosophila ananassae* flies were collected (see table 1 for abbreviations). Jammu, Dharamshala, Kangra, Dehradun, Haridwar, Mansa Devi, Gangtok, Lucknow, Guwahati, Raidopur, Chowk, Dimapur, Shillong, Patna, Allahabad, Imphal, Gaya, Ujjain, Bhopal, Indore, Jamnagar, Howarah, Sealdah, Kolkata, Rajkot, Dwarka, Ahemdabad, Paradeep, Bhubneswar, Puri, Shirdi, Nashik, Mumbai, Visakhapatnam, Vijaywada, Panaji, Madgaon, Gokarna, Manglore, Banglore, Yeswantpur, Pondicherry, Ernakulam, Thiruvananthapuram, and Kanniyakumari.

and the level of inversion heterozygosity showed north-to-south trends.

The value of D, calculated to measure the degree of genetic divergence that populations have undergone in a laboratory environment, indicated that there was variation in the degree of genetic divergence in *D. ananassae* populations transferred to laboratory conditions. Values of

Table 1. Details of collection of *Drosophila ananassae*

Name of the locality	State	Time of collection	Number of founding females
Jammu (JU)	Jammu and Kashmir	Oct. 2006	130
Dharamshala (DH)	Himachal Pradesh	Oct. 2006	46
Kangra (KG)	Himachal Pradesh	Oct. 2006	65
Dehradun (DN)	Uttaranchal	Oct. 2005	54
Haridwar (HD)	Uttaranchal	Oct. 2005	45
Mansa Devi (MD)	Uttaranchal	Oct. 2005	30
Gangtok (GT)	Sikkim	June 2006	34
Lucknow (LK)	Uttar Pradesh	Aug. 2005	48
Guwahati (GU)	Assam	June 2006	101
Raidopur (RP)	Uttar Pradesh	Sept. 2005	25
Chowk (CW)	Uttar Pradesh	Sept. 2005	71
Deemapur (DM)	Nagaland	Sept. 2006	211
Shillong (SH)	Meghalaya	June 2006	47
Patna (PN)	Bihar	Oct. 2006	211
Allahabad (AB)	Uttar Pradesh	Sept. 2005	51
Imphal (IM)	Manipur	Sept. 2006	119
Gaya (GY)	Bihar	Oct. 2006	79
Ujjain (UJ)	Madhya Pradesh	Nov. 2005	30
Bhopal (BP)	Madhya Pradesh	Nov. 2005	58
Indore (IN)	Madhya Pradesh	Nov. 2005	101
Jamnagar (JM)	Gujarat	Dec. 2005	52
Howarah (HW)	West Bengal	June 2005	35
Sealdah (SD)	West Bengal	June 2005	11
Kolkata (KL)	West Bengal	June 2005	61
Rajkot (RJ)	Gujarat	Dec. 2005	52
Dwarka (DW)	Gujarat	Dec. 2005	90
Ahemdabad (AD)	Gujarat	Dec. 2005	21
Paradeep (PA)	Orissa	May 2005	33
Bhubneswar (BN)	Orissa	May 2005	09
Puri (PU)	Orissa	May 2005	16
Shirdi (SI)	Maharashtra	June 2006	103
Nashik (NA)	Maharashtra	June 2006	134
Mumbai (MU)	Maharashtra	Jan. 2006	99
Visakhapatnam (VP)	Andhra Pradesh	June 2005	33
Vijaywada (VD)	Andhra Pradesh	June 2005	26
Panaji (PJ)	Goa	Feb. 2006	33
Madgaon (MA)	Goa	Feb. 2006	78
Gokarna (GK)	Karnataka	Feb. 2006	80
Manglore (ML)	Karnataka	Feb. 2006	118
Banglore (BL)	Karnataka	Apr. 2005	36
Yesvantpur (YS)	Karnataka	Apr. 2005	15
Pondicherry (PC)	Tamil Nadu	Apr. 2005	21
Ernakulam (ER)	Kerala	Apr. 2006	58
Thiruananthapuram (TR)	Kerala	Apr. 2006	54
Kanniyakumari (KR)	Tamil Nadu	Apr. 2006	56

D ranged from 0.006 in KG to 0.279 in BN (data not shown). The histogram based on genetic distances between initial and final populations is given in figure 2. These laboratory populations genetically diverged during their maintenance in the laboratory to greater or lesser extents. Furthermore, populations initially coming from similar environmental conditions and showing

Table 2. Frequencies (in %) of different inversions and mean number of heterozygous inversions per individual in different laboratory populations and corresponding natural populations (in parenthesis) of *Drosophila ananassae*

Population	AL	DE	ET	Mean number of heterozygous inversions per individual
JU	47.5 (61.6)	31.0 (16.2)	34.5 (15.4)	1.46 (0.923)
DH	60.5 (59.8)	43.5 (27.2)	5.0 (4.4)	1.13 (0.95)
KG	53.0 (58.5)	37.5 (39.3)	7.5 (27.3)	1.02 (0.87)
DN	100.0 (63.9)	69.0 (39.9)	0.0 (8.4)	0.38 (0.94)
HD	58.0 (48.9)	23.5 (35.6)	0.0 (6.7)	0.77 (0.84)
MD	59.5 (63.4)	4.0 (38.4)	18.0 (16.7)	0.81 (1.10)
GT	86.5 (95.6)	10.0 (14.8)	30.5 (38.3)	0.84 (0.70)
LK	34.5 (69.8)	0.0 (6.3)	1.0 (20.9)	0.51 (0.72)
GU	100.0 (92.6)	0.0 (11.4)	21.0 (36.2)	0.34 (0.78)
RP	8.0 (60.0)	0.0 (8.0)	7.0 (14.0)	0.14 (0.76)
CW	28.0 (49.3)	56.0 (11.3)	0.0 (16.2)	0.98 (0.88)
DM	81.0 (92.7)	18.5 (20.0)	7.5 (27.3)	0.76 (0.81)
SH	80.0 (97.6)	4.0 (20.8)	33.5 (28.1)	0.84 (0.73)
PN	100.0 (96.5)	15.5 (8.8)	38.0 (22.1)	0.59 (0.57)
AB	63.5 (63.8)	9.0 (18.7)	29.5 (14.8)	0.68 (1.07)
IM	91.0 (84.9)	51.0 (27.4)	24.0 (23.6)	1.20 (0.96)
GY	89.0 (96.3)	16.5 (16.5)	15.5 (23.5)	0.68 (0.74)
UJ	37.0 (68.4)	0.0 (35.0)	0.0 (16.7)	0.50 (0.86)
BP	57.5 (67.3)	10.5 (24.2)	1.0 (5.2)	0.70 (0.75)
IN	57.5 (67.3)	6.5 (38.2)	0.0 (13.4)	0.68 (1.17)
JR	92.5 (89.5)	0.0 (26.0)	4.5 (18.3)	0.18 (0.71)
HW	41.5 (75.8)	35.5 (28.6)	24.0 (5.8)	1.24 (0.77)
SD	79.5 (81.9)	28.0 (27.3)	7.0 (18.2)	0.89 (0.18)
KL	86.5 (84.5)	64.0 (31.2)	17.0 (21.4)	0.91 (0.93)
RJ	64.5 (85.6)	0.0 (24.1)	50.5 (19.3)	1.20 (0.88)
DW	100.0 (92.8)	54.5 (19.5)	21.5 (17.3)	0.82 (0.63)
AD	100.0 (95.3)	8.5 (16.7)	39.5 (16.7)	0.38 (0.47)
PA	98.5 (77.3)	19.5 (28.8)	0.0 (25.8)	0.42 (0.75)
BN	100.0 (88.9)	0.5 (38.9)	48.5 (16.7)	0.43 (0.66)
PU	62.5 (84.4)	0.0 (28.2)	26.5 (28.2)	1.08 (0.56)
SI	54.5 (85.5)	32.5 (18.5)	10.0 (11.6)	1.02 (0.58)
NA	92.5 (82.1)	30.5 (16.8)	0.0 (4.2)	0.66 (0.64)
MU	93.5 (84.9)	6.5 (10.7)	0.0 (20.3)	0.22 (0.65)
VP	77.0 (67.0)	8.5 (25.8)	42.0 (19.7)	0.99 (0.78)
VD	57.5 (67.4)	25.0 (46.2)	50.0 (36.6)	1.45 (0.76)
PJ	72.5 (92.5)	47.0 (45.5)	27.5 (15.2)	1.48 (0.81)
MA	91.0 (87.2)	0.0 (35.9)	10.5 (17.4)	1.48 (0.81)
GK	99.5 (91.3)	28.5 (60.0)	2.5 (17.5)	0.43 (0.82)
ML	60.0 (87.9)	8.5 (8.5)	41.0 (7.3)	1.03 (0.72)
BL	35.5 (68.1)	45.0 (45.9)	0.0 (25.0)	0.87 (1.38)
YS	76.0 (60.0)	47.0 (46.7)	3.0 (13.4)	1.04 (1.46)
PC	41.0 (59.6)	79.5 (50.0)	10.0 (31.0)	1.03 (1.85)
ER	75.0 (80.2)	16.5 (61.3)	27.0 (19.9)	1.05 (0.84)
TR	69.0 (85.2)	46.0 (58.4)	11.0 (14.9)	1.14 (0.90)
KR	55.5 (79.5)	91.0 (77.7)	39.0 (26.8)	1.07 (0.82)

*Total number of chromosomes examined was 200. Data given in parentheses (Singh and Singh 2007).

a high degree of similarity diverged to different degrees.

DISCUSSION

It is evident from the present observations that there is persistence of chromosomal polymorphisms due to 3 cosmopolitan inversions when *D. ananassae* populations are transferred to laboratory conditions and maintained for at least 10 generations. This finding suggests that heterotic buffering is associated with the 3 cosmopolitan inversions in *D. ananassae*. However, some populations became monomorphic for certain arrangements. The loss of a particular gene arrangement in some populations may have been due to its low frequency in the initial sample. If a particular gene arrangement initially has a low frequency, there is a greater chance of early loss due to random drift than for one with a higher frequency (Carson 1958). This assumption is supported by the observation that the highest number of populations became monomorphic for the standard gene arrangement in 3R due to loss of the eta chromosome, which occurred at a low frequency in most of the founding populations. This is quite reasonable as ET is the smallest inversion. The AL inversion, on the other hand, by virtue of being the longest among the 3 cosmopolitan inversions in *D. ananassae*, has more probability of catching 2 or more genes with a favorable epistatic effect on fitness which increases with the size of the inversion, i.e., the selective advantage gained by the inversion increases with the recombination distance between them (Càceres et al. 1999, Schaeffer et al. 2003). Further, the persistence of some inversions and the elimination of others may depend on their selective value (Brncic 1962). However, in small populations, loss or fixation occurs regardless of selection pressures (Savage 1963). Chance fixation by random drift of these gene arrangements may occur due to a high initial frequency and a possible close selective value of homozygotes to heterozygotes (Singh and Das 1992). Carson (1961) predicted that the increase in the frequency of the new gene arrangement may be due either to some selective advantage of the arrangement conferred on those individuals carrying it or to its linkage with a gene arrangement already participating in a major heterotic association. However, the failure of a majority of populations to become chromosomally homozygous suggests that the heterozygotes due to AL (2L), DE (3L), and ET (3R) inversions in *D. ananassae* are adaptively superior to their corresponding homozygotes (see Tobari 1993 for references). It could also be stated that a random process of change in gene frequencies may involve the Markov property in the sense that changes in gene frequencies in a given population depend solely on their frequency in the immediately preceding generation and are totally independent of the past history of the populations

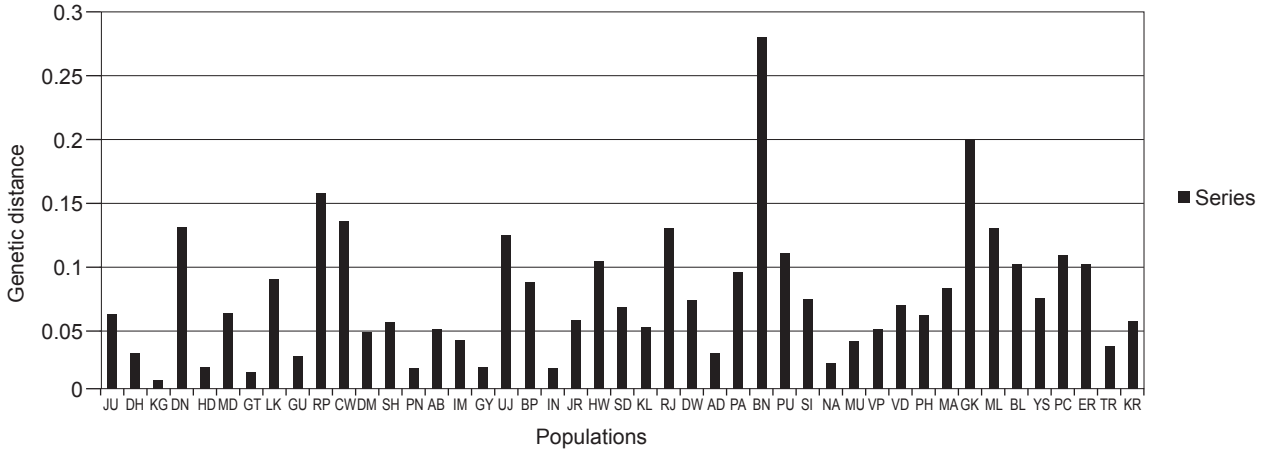

Fig. 2. Histogram showing genetic distances between initial and final populations of *Drosophila ananassae* (see table 1 for abbreviations). Jammu, Dharamshala, Kangra, Dehradun, Haridwar, Mansa Devi, Gangtok, Lucknow, Guwahati, Raidopur, Chowk, Dimapur, Shillong, Patna, Allahabad, Imphal, Gaya, Ujjain, Bhopal, Indore, Jamnagar, Howarah, Sealdah, Kolkata, Rajkot, Dwarka, Ahemdabad, Paradeep, Bhubneswar, Puri, Shirdi, Nashik, Mumbai, Visakhapatnam, Vijaywada, Panaji, Madgaon, Gokarna, Manglore, Banglore, Yeswantpur, Pondicherry, Ernakulam, Thiruvananthapuram, and Kanniyakumari.

(Narain 1990).

A comparison of frequencies of different chromosome arrangements between natural and laboratory populations showed that there were considerable changes in certain populations. However, some populations maintained more or less similar frequencies. For instance with respect to AL inversion, DH-60.5 (59.8), KG-53.0 (58.5), MD-59.5 (63.4), PN-100.0 (96.5), AB-63.5 (63.8), JR-92.5 (89.5), SD-79.5 (81.9), KL-86.5 (84.5), DW-100.0 (92.8) and AD-100.0 (95.3). For delta inversion, KG-37.5 (39.3), GT-10.0 (14.8), DM-18.5 (20.0), GY-16.5 (16.5), SD-28.0 (27.3), PJ-47.0 (45.5), ML-8.5 (8.5), BL-45.0 (45.9) and YS-47.0 (46.7); while for eta inversion, DH-5.0 (4.4), MD-18.0 (16.7), IM-24.0 (23.6), PU-26.5 (28.2) and SI-10.0 (11.6). Thus, the results reported herein do not support the hypothesis of Lewontin (1957) that polymorphism should be lost in a uniform environment or the ecological niche hypothesis of Da Cunha and Dobzhansky (1954) that the degree of inversion polymorphism is an index of environmental heterogeneity. On the other hand, it reinforces the idea of Carson (1961) that genetic polymorphism may be lost in a uniform environment only if each heterozygote is especially adapted in nature to some slightly different environmental variable which is not present in laboratory conditions. Random associations appearing in founder populations may well result in a conversion of the selection process that would induce founder populations to end up with gene pool compositions different from those of the original main populations (Sperlich et al. 1982).

A histogram showing genetic distances between natural and laboratory populations and values of D indicate that there is variation in the degree of genetic divergence in *D. ananassae* populations transferred to laboratory conditions. Some populations have diverged genetically during their maintenance in the laboratory but to a greater or lesser extent. Populations coming from similar environmental conditions and initially showing a high degree of genetic similarity diverged to different degrees. The degree of genetic differentiation between natural and laboratory populations differed. Variations in the degree of genetic divergence in *D. ananassae* populations cannot simply be explained by the process of genetic reconstruction in view of drastic environmental changes that a population suffered when it was moved to laboratory conditions. This change can be attributed to genetic drift. This seems more plausible as populations were maintained in culture bottles by transferring nearly 50 flies each generation. Operation of genetic drift in laboratory populations causes significant differences in the frequencies of different chromosome arrangements of *D. ananassae* (Singh 1987 1988). It can also be said that populations that have spent more generations in the laboratory have diverged more than populations that have been maintained for fewer generations (Fig. 2). This is because with an increasing number of generations, the probability increases of genetic drift causing fixation of a particular gene arrangement on account of its high initial frequency or eliminating others due to their low frequencies. This is particularly true when small-sized populations are maintained in culture bottles in the laboratory.

Laboratory experiments, performed to emphasize the role of recombination in providing adaptive flexibility, have shown that populations that are monomorphic for inversions respond more quickly to selective pressures than do polymorphic populations, thus indicating the role of recombination in allowing a population to respond to selection (Carson 1958, Markow 1975, Tabachnick and Powell 1977). Because of this selection, the genotype on which it acts will come to attain different adaptive peaks than that occupied by parental populations, thus leading to divergence (Powell 1997).

Establishing laboratory stocks is always accompanied by a reduction in genetic variation of the sample giving rise to founder effects (Pinsker 1981). Since these lines were maintained by transferring a smaller number of flies than the total number of flies hatched in the bottles, the changes observed in the frequencies of chromosomes are likely to have been caused by genetic drift (Singh 1988). In small populations, sampling errors may cause the gene frequency in the next generation to be higher or lower than in the preceding generation. The smaller the population is, the more appreciable the sampling errors will be, and in successive generations, the sampling errors are likely to accumulate. It stands to reason that random genetic drift can diversify an array of initially genetically identical but isolated populations without intervention of natural selection (Dobzhansky et al. 1976). Furthermore, the periodic transfer of about 50 flies from an old culture bottle to a fresh culture bottle was used to maintain the laboratory populations in each generation. Therefore, in polymorphic culture, genetic variants are exposed in each generation to

the risk of not being included among the parents of the succeeding generation. Following this breeding system to maintain populations for such a long time, the populations should have become homozygous due to the loss of unfixed genetic variants. Tobari (1993), on the basis of estimated fitness of the karyotypes, demonstrated that the joint effect of frequency-dependent selection and heterozygote superiority seems very likely to be responsible for frequency changes observed in laboratory populations.

Among different elemental forces of evolution, natural selection and genetic drift are important in causing alterations in gene frequencies in populations. In a given environment, certain alleles or gene combinations may be favored due to high adaptive values of their carriers by selection, which leads to a gradual enhancement in the frequencies of those alleles in the population. However, in small populations, gene frequencies may significantly fluctuate due to random genetic drift. The occurrence of selection and drift has been demonstrated in many cases. Thus, it can be suggested that variations in the degree of genetic differentiation in *D. ananassae* populations when moved to laboratory conditions are likely to be due to genetic drift though inversions in this species are subject to selection.

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REFERENCES

Brncic D. 1962. Chromosomal structure of populations of *Drosophila flavopilosa* studied in larvae collected in their natural breeding sites. Chromosoma **13:** 183-195.

Càceres M, A Barbadilla, A Ruiz. 1999. Recombination rate predicts inversion size in Diptera. Genetics **153:** 251-259.

Carson HL. 1958. Response to selection under different conditions of recombination in *Drosophila*. Cold Spring Harbor Symp. Quant. Biol. **23:** 291-306.

Carson HL. 1961. Relative fitness of genetically open and closed experimental populations of *Drosophila robusta*. Genetics **46:** 553-567.

Da Cunha AB. 1960. Chromosomal variation and adaptation in insects. Annu. Rev. Entomol. **5:** 85-110.

Da Cunha AB, T Dobzhansky. 1954. A further study of chromosomal polymorphism in *Drosophila willistoni* in its relation to environment. Evolution **8:** 119-134.

De Frutos R. 1978. Changes of chromosomal polymorphism in experimental cage populations of *Drosophila subobscura*. Genetica **49:** 139-151.

Dobzhansky T. 1970. Genetics of the evolutionary process. New York: Columbia Univ. Press.

Dobzhansky T, FJ Ayala, GL Stebbins, JW Valentine. 1976. Evolution. Delhi: Surjeet Publications.

Dobzhansky T, NP Spassky. 1962. Genetic drift and natural selection in experimental populations of *Drosophila pseudoobscura*. Proc. Natl. Acad. Sci. USA **48:** 148-156.

Inoue Y. 1979. The fate of polymorphic inversions of *Drosophila melanogaster* transferred to laboratory conditions. Jpn. J. Genet. **54:** 83-96.

Krimbas CB, M Loukas. 1980. The inversion polymorphism of *Drosophila subobscura*. Evol. Biol. **12:** 163-234.

Levene H, T Dobzhansky. 1958. New evidence of heterosis in naturally occurring inversion heterozygotes in *Drosophila pseudoobscura*. Heredity **12:** 37-49.

Lewontin RC. 1957. The adaptations of populations to varying environments. Cold Spring Harbor Symp. Quant. Biol. **22:** 395-408.

Markow TA. 1975. A genetic analysis of phototactic behavior in *Drosophila melanogaster*. I. Selection in the presence of inversions. Genetics **79:** 527-534.

Narain P. 1990. Statistical genetics. New Delhi: Wiley Eastern.

Nei M. 1972. Genetic distance between populations. Am. Nat. **106:** 283-292.

Pinsker W. 1981. MDH polymorphism in *Drosophila subobscura*. I. Selection and hitch-hiking in laboratory populations. Theor. Appl. Genet. **60:** 107-112.

Powell JR, ed. 1997. Progress and prospects in evolutionary biology. The *Drosophila* model. New York: Oxford Univ. Press.

Powell JR, RC Richmond. 1974. Founder effects and linkage disequilibrium in experimental populations of *Drosophila*. Proc. Natl. Acad. Sci. USA **71:** 1663-1665.

Richardson RH, JS Yoon. 1973. Technique for improving salivary chromosome preparations. Experientia **29:** 639-641.

Savage JM. 1963. Evolution. New York: Holt, Rinehart and Winston.

Schaeffer SW, MP Goetting-Minesky, M Kovacevic, JR Peoples, JL Graybill, JM Miller, K Kim, JG Nelson, WW Anderson. 2003. Evolutionary genomics of inversions in *Drosophila pseudoobscura*, evidence for epistasis. Proc. Natl. Acad. Sci. USA **100:** 8319-8324.

Singh BN. 1972. The lack of evidence for coadaptation in geographic populations of *Drosophila ananassae*. Genetica **43:** 582-588.

Singh BN. 1974. Persistence of heterosis in crosses between geographic races of *Drosophila ananassae*. Ind. J. Exp. Biol. **12:** 376-377.

Singh BN. 1981. Interracial hybridization in *Drosophila ananassae*. Genetica **57:** 139-142.

Singh BN. 1982. Persistence of chromosomal polymorphism in various strains of *Drosophila ananassae*. Genetica **59:** 151-156.

Singh BN. 1983a. Cosmopolitan inversions in *Drosophila ananassae*. Caryologia **36:** 333-343.

Singh BN. 1983b. Variation in gene arrangement frequencies and the degree of heterosis in laboratory strains of *Drosophila ananassae*. Braz. J. Genet. **6:** 407-414.

Singh BN. 1985. Heterosis without selectional coadaptation in *Drosophila ananassae*. Theor. Appl. Genet. **69:** 437-441.

Singh BN. 1987. On the degree of genetic divergence in *Drosophila ananassae* populations transferred to

laboratory conditions. Zeit. Zool. Syst. Evol. **25:** 180-187.
Singh BN. 1988. Evidence for random genetic drift in laboratory populations of *Drosophila ananassae*. Ind. J. Exp. Biol. **26:** 85-87.
Singh BN. 1998. Population genetics of inversion polymorphism in *Drosophila ananassae*. Ind. J. Exp. Biol. **36:** 739-748.
Singh BN. 2001. Patterns of inversion polymorphism in three species of the *Drosophila melanogaster* species group. Ind. J. Exp. Biol. **39:** 611-622.
Singh BN, R Banerjee. 1997. Increase in the degree of inversion polymorphism in *Drosophila bipectinata* populations transferred to laboratory conditions. J. Zool. Syst. Evol. Res. **35:** 153-157.
Singh BN, A Das. 1992. Changes in inversion polymorphism in laboratory populations of *Drosophila melanogaster*. Zeit. Zool. Syst. Evol. **30:** 268-280.
Singh P, BN Singh. 2004. Genetic differentiation among laboratory populations of *Drosophila ananassae* established from naturally impregnated females. Proc. Zool. Soc. **57:** 105-117.
Singh P, BN Singh. 2007. Population genetics of *Drosophila ananassae*: genetic differentiation among Indian natural populations at the level of inversion polymorphism. Genet. Res. **89:** 191-199.
Sperlich D. 1973. Populationsgenetik. Stuttgart: G. Fischer.
Sperlich D, A Karlik, P Pfriem. 1982. Genetic properties of experimental founder populations of *Drosophila melanogaster*. Biol. Zbl. **101:** 395-441.
Sperlich D, W Pinsker, AZ El-Abidin Salam. 1976. A stable enzyme polymorphism associated with inversion polymorphism in laboratory strains of *Drosophila subobscura*. Egypt. J. Genet. **5:** 153-163.
Spiess EB. 1950. Experimental populations of *Drosophila persimilis* from an altitudinal transect of Sierra Nevada. Evolution **4:** 14-33.
Spiess EB. 1957. Relation between frequencies and adaptive values of chromosomal arrangements in *Drosophila persimilis*. Evolution **11:** 84-93.
Strickberger MW. 1962. Experiments in genetics with *Drosophila*. New York: J Wiley.
Tabachnick WJ, JR Powell. 1977. Adaptive flexibility of “marginal” versus “central” populations of *Drosophila willistoni*. Evolution **31:** 692-694.
Tobari YN, ed. 1993. Population genetics. *In Drosophila ananassae*, genetical and biological aspects. Tokyo: Japan Scientific Societies Press, pp. 139-192.
Watanabe TK, WW Anderson, T Dobzhansky, O Pavlovsky. 1970. Selection in experimental populations of *Drosophila pseudoobscura* with different initial frequencies of chromosomal variants. Genet. Res. **15:** 123-129.