Inversion and isozyme variation, mating behavior, and fitness in *Drosophila ananassae*.

Jayaramu, S.C.*, and M. Prathibha. Department of Zoology, Yuvaraja's College, University of Mysore, Mysore 570005, Karnataka State, India. *corresponding author - E-mail: jayaramu21@gmail.com; prathibhajayaramu@gmail.com.

Abstract

Natural populations are endowed with a large amount of chromosomal and genetic variation. In the present study, we have tried to find out whether any correlation between different polymorphisms exists. For this purpose, **i**nversion frequencies and α-esterase variation were studied in four different populations of *D. ananassae* collected from Dharwad, Bellur, Krishnarajanagar and Mysore, India. Present study has demonstrated high polymorphism of both inversions and α-esterase. The role of inversions and α-esterase phenotypes on mating behavior and fitness has also been studied. Three different strains of *D. ananassae* carrying 2LA, 3LA and 2LA+3LA inversions and one inversion free strain were built up in the laboratory using the female flies collected from natural habitat at Mysore, India. Mating behaviors, such as courtship latency, mating latency, and copulation duration, and fitness characters, such as fecundity, viability, and fertility, were studied in these inversion and inversion-free stocks using no choice experiment. The mating behaviors and isozyme pattern in three different inversions and inversion-free strains of *D. ananassae* were quantified and compared between different strains. The carrier of two inversions (2LA+3LA) took more time to copulate but had higher fitness than inversion-free stock or stock carrying single inversion. The concept of inversion heterokaryotype superiority is confirmed with reference to both inversion and α-esterase polymorphism.

Introduction

One of the most important aspects of evolutionary biology is the study of how natural selection modifies the genetic structure of populations. For this to happen, populations must encompass some degree of chromosomal or genetic variation or other kinds of modifications in the gene pool. Analysis of inversion polymorphism is one of the strategies to know the extent of genetic variation between populations. Such an analysis has been made extensively in many species of *Drosophila* (Krimbas and Powell, 1993). The early studies on inversion polymorphism have also demonstrated the superiority of inversion heterokaryotypes over homokaryotypes (Singh and Chatterjee, 1986). Genetic variation at allozyme loci has also been studied in *Drosophila* (Barker, 1981). A combination of these two kinds of analyses has demonstrated the association between inversion and allozyme polymorphism (David, 1982). Non-random association between allozymes and inversions in natural populations of *D. melanogaster* has been demonstrated by Langley *et al.* (1977). Over dominance at different isozyme loci and linkage disequilibrium among multiple neutral alleles was also demonstrated (Hill, 1975). Barker and Mulley (1976) have demonstrated that out of six allozyme loci which are consistently polymorphic in Australian populations of *D. buzzatii*, three (esterase-1, esterase-2, and aldehyde oxidase) are linked with chromosomal inversions. Knibb *et al.* (1987) also found that esterase locus is tightly linked to an inversion complex in *D. buzzatii*. Thus the available literature amply supports the existence of association between inversion polymorphism and allozyme polymorphism.

Studies on different aspects of sexual, non-sexual behavior, and fitness in various species of *Drosophila* have also been well documented (Smith, 1956; Sisodia and Singh, 2005). Mating behavior of *Drosophila* consists of specific actions which are accompanied by orientation movements. Such actions referred to as courtship displays are made up of several signals which are performed sequentially. Mating occurs only if the female responds by performing acceptance signals. Since sexual behavior of males and females affects and modifies the contribution of different genotypes to the gene pool of succeeding generations, it becomes an important component of fitness. In *Drosophila*, successful mating depends on male activity and female receptivity because usually the female is the discriminating partner in the mating act, *i.e*., she actively accepts or rejects a courting male (Bastock, 1956).

Mating speed (or courtship time), the time from the beginning of courtship to copulation (Spieth and Ringo, 1983), is a good estimate of sexual receptivity of females and sexual activity in males. It is known that male activity and female receptivity are the main factors responsible for successful mating in *Drosophila* (Bastock, 1956). A considerable amount of information on genetic determination of sexual behavior in *Drosophila* is available (Singh and Singh, 1999). Investigations on mating propensity in various species of *Drosophila* (Spiess, 1970) have also shown that efficiency of mating varies for different genotypes. The contribution of males to the variation in mating propensity is greater than that of females and thus males are inherently more subject to intrasexual selection (Parsons, 1965; Singh and Chatterjee, 1987). However, Kessler (1968) reported that females contribute more to the variation of mating speed than males of *D. pseudoobscura*. From previous reports on sexual behavior in the genus *Drosophila*, it is clear that the efficiency of mating differs in different genotypes (Smith, 1956; Sisodia and Singh, 2001).

In addition to inversions, isozyme variants also have influence on sexual behavior and fitness. Although vast literature is available, no effort has been made to correlate between each of these parameters. The question is whether inversion polymorphism and / or enzyme polymorphism, sexual behavior and fitness are interrelated or independent of one another? Whether inversion polymorphism has any influence on the expression of allozyme alleles? What is the role of inversion or allozyme polymorphism on these traits? In the present studies, the authors have tried to address the above questions. For this purpose *D. ananassae* has been selected as the experimental model because of its following characteristics. It is a cosmopolitan domestic species belonging to *melanogaster* group of *ananassae* subgroup and *ananassae* species complex (Bock and Wheeler, 1972). This species occupies a unique status in the whole of genus *Drosophila* due to certain peculiarities in its genetical behavior (Singh, 1985). Absence of male crossing over, high level of inversion polymorphism, and high mutability are the features which make it useful for certain genetic studies. Although the species harbors large number of inversions, most of the inversions are found in isolated populations. One interesting feature of inversion polymorphism of this species is that it carries three well-knit co-extensive inversions found in geographic populations. They are 2LA, on the left arm of the 2nd chromosome, 3LA on the left arm of the 3rd chromosome, and 3RA on the right arm of the 3rd chromosome. The frequency of these inversions varies in different geographical populations and, hence, they can be subjected to different types of genetic analysis on inversions.

Materials and Methods

Analysis of inversion frequencies in natural populations:

D. ananassae flies collected from Dharwad, Bellur, Krishnarajanagar and Mysore following the procedure described by Hegde *et al.* (1999) were used for the present study. After the flies were

brought to the laboratory, the females were individually placed in glass vials (2.5 cm × 8.5 cm) containing wheat cream agar medium, and males were used for identification and for analysis of α-esterase polymorphism. The female flies were then maintained at constant temperature of 22 ± 1°C and relative humidity of 70%. When larvae appeared, eight third instar larvae from each isofemale line were used for analysis of inversion frequency and others were allowed to continue their development. The inversion frequency was studied by polytene chromosome preparation following the procedure described by Reddy and Krishnamurthy (1974).

Analysis of α-esterase variation in natural populations:

The same four populations used for analysis of inversion polymorphism were also used for analyzing the α-esterase polymorphism. This was intended to understand the extent of α-esterase variation present in the natural population. For this purpose, the wild caught males and the females of the F_1 progeny of wild caught females of the same four natural populations of *D. ananassae* employed above were used. Single fly homogenates were used as sample and electrophoresed separately. The polyacrylamide gel electrophoretic technique described by Davis (1964) modified for vertical slab gel was used. The gels were stained for α-esterase using the staining procedure described by Hegde and Krishnamurthy (1976).

Calculation of allelic frequencies:

After electrophoresis, the zymograms were drawn for each individual and used for calculation of allelic frequencies. To identify the alleles and to assign the locus to which they belong, a cross was conducted between individuals of F1 progeny of wild caught females and the pattern of segregation of different bands was analyzed. Accordingly three loci were recognized for α- which were designated as α-esterase α-est1, α-est-2, α-est-3. On the basis of mobility two alleles in each locus, *viz*., fast (F) and slow (S) were recognized. When there was a single band at a given locus (either F or S), then the individual was considered as homozygote for that locus and if there were two bands together (both F and S), then it was considered as a heterozygote. To calculate the allelic frequencies – as per the Hardy-Weinberg equilibrium, half of the total number of heterozygotes observed is added to the homozygotes scored and this value is divided by the total number of genomes (N) sampled. Further, Z-Statistics (H) was calculated using the formula $H = 1 - \sum p_i^2$, where p is the frequency of the i'th allele at the given locus and $\sum$ is the summation of the over all F and S alleles.

Establishment of inversion stocks:

To analyze the role of inversions on mating behavior and isozyme pattern, three different strains carrying 2LA, 3LA, and 2LA+3LA inversions and one inversion free strain were built up in the laboratory using the female flies collected from natural habitat at Mysore. For the sake of convenience, these strains were designated as IA, IB, IC, and ID, respectively. IA is monomorphic (inversion free), IB is with 2LA, IC is with 3LA, and ID is with 2LA+3LA strains. These females were individually placed in vials containing wheat cream agar media (isofemale line) and when larvae appeared, eight larvae from each vial were sacrificed to check for presence or absence of inversions in their salivary gland chromosomes. The cytological detection of these inversions was made using the procedure of Rajeshwari and Krishnamurthy (1969). *D. ananassae* populations collected from Mysore carries two common inversions namely, 2LA and 3LA. The wild caught individuals, therefore, would be either without inversion or carry 2LA alone, or 3LA alone, or both 2LA+3LA. When all the eight larvae carried a given inversion, then that individual (their mother)

was designated as the strain carrying that particular inversion. The adult progenies which appeared from such mothers were classified as inversions free, 2LA, 3LA, and 2LA+3LA strains.

These strains were separately maintained for six generations and at each generation, three to five larvae were used to check for the presence or absence of respective inversions. Although in each generation, the polytene chromosomes showed the presence of either inversion loop or absence of loop, because they originate from same isofemale line, all progeny contained only that particular inversion homokaryotype or heterokaryotype. The adults emerged from these strains were used to build up populations for the study of variation in mating behavior, fitness, and isozymes.

Analysis of mating behaviour and fitness among four inversion phenotypes:

To study the mating behavior of the four inversion phenotypes, virgin females and bachelor males from each inversion line were isolated within three hours of eclosion from stocks developed as above and were kept separately for the study of mating behavior. They were aged for 5 days; then a virgin female along with a bachelor male was placed in an Elens-Wattiaux mating chamber (a circular chamber with a diameter of 9 cms). Each pair was observed for 1 hr and if there was no mating, then the pair was discarded. For each mating pair, courtship latency (time between introduction of male and female together into mating chamber until orientation of male towards female - usually measured in seconds), mating latency (time between introduction of male and female together into mating chamber until initiation of copulation of each pair – measured in minutes) and copulation duration (time between the initiation of copulation to termination of copulation of each pair – measured in minutes) were observed following the procedure of Hegde and Krishna (1997). A total of 30 pairs were observed in this way and the means and standard errors were calculated. To analyze fitness, each mated pair was transferred into a vial containing wheat cream agar medium. After 24 hours, the pairs were transferred to fresh food vial, and the eggs laid in the previous vial were counted. This procedure was continued for 15 days, and the total number of eggs laid and the adults emerged from each pair was recorded to determine fecundity, viability, and fertility of these strains. The data were statistically analyzed by One-way ANOVA followed by DMRT.

Analysis of α-esterase variation in the four inversion phenotypes:

The variations of α-est in four strains were studied here by homogenizing the flies individually in 40% sucrose solution and kept separately. Electrophoresis was carried out as per the procedure described above. The zymograms were drawn for each individual for α-est of all the four inversion strains.

Results

Variation inversion and α- esterase isozymes in natural populations:

Table 1 shows percentage of different inversions present in different geographical populations of *D. ananassae.* It was noticed that the frequency of inversions differ in different geographical populations. In all populations, the highest number of individuals carried 3LA inversion while the least number of individuals was inversions free. Figure 1 shows the zymogram of α-esterases found in four different populations of *D. ananassae*. Three loci were identified at α-esterase locus, each with two alleles, F and S. Table 2 shows the allelic frequencies of alpha esterase (α-est) isozymes of four different natural populations. The frequencies of slow moving allele (S) of α-est-1 were less than the frequencies of the corresponding fast moving alleles in all the four populations studied. In the α-est-1 locus, the frequency of slow moving allele of Dharwad population was lowest while that

of Mysore population was highest. The χ^2 values calculated for the percentage of slow moving allele present in different populations show that the allelic frequencies between populations were significant. Correspondingly, the frequency of fast moving allele of Mysore population was highest and of Dharwad population was lowest. Further, the H value calculated on the basis of Z-statistics showed that Mysore population is more polymorphic than others.

Table 1. Inversion frequency (%) in different geographic populations of *D. ananassae.*

Strains	Inversion frequency (%)				
	N	2LA	3LA	2LA+3LA	Inversion free (Monomorphic)
Bellur	32	16.7	40.0	26.7	16.6
Dharwad	38	20.0	50.0	20.0	10.0
Krishnarajanagar	42	36.7	53.3	06.7	03.3
Mysore	40	33.3	43.4	10.0	13.3

Table 2. Allelic frequencies at α-est loci in different populations of *D. ananassae.*

Locus	Allele	Dharwad	Krishnarajanagar	Mysore	Bellur	χ^2-value
α-est-1	Slow	0.19	0.32	0.33	0.29	20.84*
	Fast	0.81	0.68	0.67	0.71	13.07*
H		0.31	0.43	0.44	0.41	
N		38	42	40	32	
α-est-2	Slow	0.95	0.81	0.84	0.85	11.33*
	Fast	0.05	0.19	0.14	0.15	28.11*
H		0.95	0.30	0.27	0.25	
N		38	42	40	32	
α-est-3	Slow	0.84	0.76	0.72	0.80	10.09*
	Fast	0.16	0.24	0.28	0.20	19.05*
H		0.26	0.52	0.40	0.32	
N		38	42	40	32	

*χ^2 values are significant at 0.05 levels.

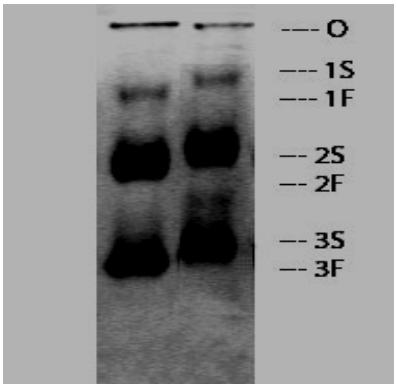

Figure 1. Showing the α-est loci found in the natural populations of *D. ananassae.* (O = Origin, F and S are the alleles of the three loci).

Contrary to the α-est-1 locus, the slow moving alleles in α-est-2 and α-est-3 were found to be more than the fast moving allele. The frequency of the slow moving allele of α-est-2 locus ranged from 0.81 in Krishnarajanagar population to 0.95 in Dharwad population. Similarly the frequency of fast moving allele ranged from 0.05 in Dharwad to 0.19 in Krishnarajanagar population.

The χ^2 values calculated for these allelic frequencies showed significant differences between different populations at 0.05 levels. The H value showed that even with regard to α-est-2 locus all the four populations analyzed were polymorphic. In α-est-3 locus, the slow moving allele had a frequency ranging from 0.72 in Mysore to 0.84 in Dharwad population. On the other hand the fast moving allele of Dharwad was represented with a low frequency of 0.16 and Mysore population had the frequency of 0.28. Corresponding with allelic frequencies, the H value also varied between different populations.

Table 3. Mating behavior, fecundity, viability and fertility of different inversion strains of *D. ananassae* (Values are Mean ± SE).

Strain → ↓Parameters value	IA (Inversion free)	IB (2LA inversion)	IC (3LA inversion)	ID (2LA+3LA Inversion)	F
Courtship latency (in seconds)	50.13 ± 3.44[a]	46.73 ± 4.25[a]	41.66 ± 3.00[a]	69.93 ± 5.78[b]	08.45**
Mating latency (in minutes)	27.92 ± 2.72[a]	24.41 ± 2.99[a]	26.08 ± 3.19[a]	28.60 ± 3.30[a]	11.78**
Copulation duration (in minutes)	3.76 ± 0.14[a]	4.08 ± 0.18[b]	3.60 ± 0.13[a]	4.11 ± 0.10[b]	2.99*
Fecundity (in nos)	45.53 ± 4.81[a]	57.53 ± 5.33[a]	122.06 ± 5.35[b]	131.53 ± 11.95[b]	49.10**
Viability (in nos) (No.of larvae/100 eggs)	42.06 ± 1.19[b]	36.66 ± 0.91[a]	79.10 ± 2.42[c]	94.26 ± 2.00[d]	259.35**
Fertility (in nos)	31.53 ± 4.15[a]	24.26 ± 2.76[a]	69.80 ± 9.93[b]	83.86 ± 11.88[b]	12.68**

IA, IB, IC and ID are α-esterase phenotypes (refer Fig. 2)
Same superscript in each row indicates that the value is nonsignificant by DMRT.
*P< 0.005, **P< 0.001.

Variation in mating behavior and fitness of inversion phenotypes:

Table 3 shows mating behavior, fecundity, viability, and fertility of different strains of *D. ananassae*. It is noticed that courtship latency was highest in the strain with double inversion (ID) while it was lowest in the 3LA (IC) strain. One way ANOVA followed by DMRT applied on mean courtship latency of different strains showed that mean courtship latency varied significantly between them. The mean mating latency of different strains of *D. ananassae* is also provided in Table 3. It is noticed that mating latency was highest in strain 2LA+3LA (ID), while it was lowest in the 2LA (IB) strain. Although the analysis of variance showed significant differences between different strains, by DMRT these differences were found to be non-significant. Mean copulation duration of different inversion strains revealed that mean copulation duration was highest in strain 2LA+3LA (ID) (value significant over all others) while lowest in 3LA (IC) strain. The application of ANOVA followed by DMRT showed that the mean copulation duration of inversion free (IA) strain was significantly less than 2LA (IB) and 2LA+3LA (ID) strains but non-significant with 3LA (IC).

Mean fecundity of different strains is provided in Table 1. It was noticed that fecundity was highest in 2LA+3LA (ID) strain and lowest in inversion free (IA) strain. The data on mean fecundity subjected to one way ANOVA followed by DMRT showed significant variation in fecundity between different strains. DMRT showed that mean fecundity of inversion free strain was significantly less with all other strains. Thus the mean fecundity of different inversion strains in the decreasing order was, inversion free < 2LA < 3LA < 2LA+3LA. It was noticed that viability was highest in 2LA+3LA (ID) strain and lowest in 2LA (IB) strain. The data on mean viability subjected to one way ANOVA followed by DMRT showed significant variation in viability between different strains. DMRT showed that mean viability of 2LA (IB) strain was significantly less with all other strains. Thus the mean viability of different inversion strains in the decreasing order was, 2LA < inversion

free < 3LA < 2LA+3LA. Further, highest fertility was noticed in 2LA+3LA (ID) strain and least in 2LA (IB) strain.

Mean fertility data when subjected to one way ANOVA followed by DMRT showed significant variation in fertility between different strains. DMRT showed that mean fertility of inversion free (IA) strain was significantly less than 3LA (IC) and 2LA+3LA (ID) strains but non-significant with the 2LA (IB) strain. In summary, the mean fertility of different inversion strains in the decreasing order was, 2LA < inversion free < 3LA < 2LA+3LA.

Variation of α-est isozymes in the four inversion phenotypes:

Figure 2 shows the variation of α-est isozymes in the inversion free strain and different inversion strains. The IA (inversion free) strain carried only two bands, representing α-est-2F and α-est-3F. The IB (2LA inversion) strain also showed two bands but representing α-est-2S and α-est-3S. Similarly the IC (3LA inversion) strain had α-est-2S and α-est-3S. The ID (2LA and 3LA inversions) strain had three bands representing α-est-1F, α-est-2S, and α-est-3S.

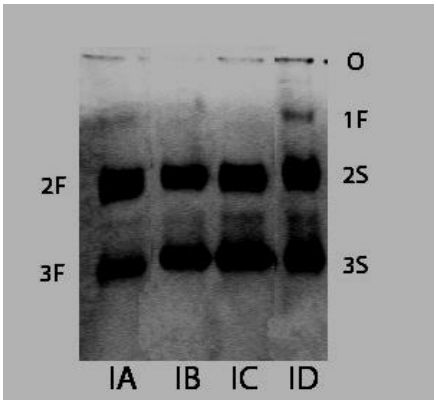

Figure 2. Showing the α-est loci found in different inversion strains of *D. ananassae.* (IA = Inversion free, IB = 2LA inversion, IC = 3LA inversion and ID = 2LA+3LA inversion strains).

Discussion

Variation inversion and α-esterase isozymes:

The study of inversion and α-esterase polymorphism in four natural populations of *D. ananassae* shows high polymorphism of both these parameters (Tables 1 and 2). Both 2LA and 3LA were present in these populations with varying frequencies. This observation agrees with the findings of Reddy and Krishnamurthy (1974), who have also demonstrated variation in the frequencies of 2LA and 3LA inversions in certain South Indian populations of *D. ananassae*. There are three α-esterase loci in the four populations of *D. ananassae* and all these loci were found to be polymorphic (Figure 1). There are a number of such studies, which demonstrate the inversion and isozyme studies (Johnson, 1971; Barker and Mulley, 1976). Our study also confirms the existence of high polymorphism in natural populations of *D. ananassae*.

In the present studies, the authors have tried to correlate the enzyme variation with chromosomal inversions. It is found that the inversion free (IA) strain showed only two esterase (isozymes) forms α-est-2F and α-est-3F (Figure 2). The 2LA (IB) inversion strain also showed two isozymes but representing α-est-2S and α-est-3S. Similarly the strain carrying inversion 3LA (IC) had α-est-2S and α-est-3S. The inversion strain carrying both 2LA and 3LA together (ID) had three isozymes representing α-est-1F, α-est-2S, and α-est-3S. Thus more alleles expressed in the double inversion strain compared to others. This indicates the heterotic effect even with reference to the expression of isozymes in *D. ananassae*. The study thus agrees with those of Zouros and Johnson

(1976) who while demonstrating allozyme variation also found heterotic effect at certain loci in *D. buzzatii*.

In *D. ananassae*, the α-esterase gene complex is located on left arm of the second chromosome in scaffold 13340 in the Muller's element E. The authors have noticed that the inversion phenotypes 2LA and 3LA have the same pattern of expression of α-esterase (see Figure 2). This means carrying these inversions has no effect on the expression of α-esterase alleles.

Based on the distribution, Mettler *et al.* (1977) classified the inversions of *D. melanogaster* as cosmopolitans, which occur in many populations often at frequencies greater than 5%, and rare cosmopolitans, which are present in many populations but at frequencies usually less than 5%. Recurrent endemics are those that occur in only few individuals in the same or adjacent populations, while unique endemics are those recorded only once. Knibb *et al.* (1987) have demonstrated lower esterase activity due to linkage disequilibrium of these loci on the second chromosome of *D. buzzatii* associated with certain cosmopolitan inversions. In *D. ananassae*, the two inversions, 2LA and 3LA, are cosmopolitans because they occur in most of the populations at frequency greater than 5% (Futch, 1966; Reddy and Krishnamurthy, 1974). Even in the present study the four populations in which the inversion frequencies have been estimated, they exist at high frequency (Table 3). If inversion has an effect on the expression of α-esterase there should have been a difference in the expression pattern between the inversion strains. However, no such difference in α-esterase pattern was noticed by the authors between 2LA (IB) and 3LA (IC) strains. Thus the present study demonstrates that these inversions have no effect on the esterase alleles.

Variations in courtship acts and fitness:

In *Drosophila* many adaptive functions have been found to be associated with inversion polymorphism. The present study demonstrates that the courtship acts and fitness are associated with inversion polymorphism. Courtship latency is one of the parameters that indicate vigor of a male (Singh and Singh, 1999; Sisodia and Singh, 2001). A male with high vigor reacts quickly in the presence of female, while a male with less vigor reacts slowly (Markow, 1978). Mating latency indicates both vigor of males and receptivity of females. Higher the vigor of males and receptivity of females, shorter is the mating latency. During this period, courtship acts are performed mostly by males, to increase the receptivity of females and to make her sexually excited (Spieth, 1968). A male with high vigor has to perform the same courtship act more times to a non-receptive female than to a receptive female. Correspondingly when a female is receptive, males' activity may be brief and he may mate her more quickly than a non-receptive female. In the present studies, both courtship and mating latency were highest in the double inversion strain (2LA+3LA) than others. This means carrying two inversions reduces the vigor of males and receptivity of females. However, the copulation duration was highest in the double inversion strain than others. During copulation sperm from the male is transferred to the female reproductive tract and, therefore, the duration of copulation has a lot of significance in an animals' life. Since increased copulation duration increases the number of ejaculations, longer copulation duration is more advantageous at least for animals with limited number of matings during their lifespan. Many workers have demonstrated heterotic effect of inversion polymorphism in both laboratory and natural populations of *Drosophila* (Singh and Chatterjee, 1986; Krimbas, and Powell, 1993) with reference to the fitness. The present study thus demonstrates the heterotic effect with regard to copulation duration also. The purpose of courtship is to transfer maximum number of sperms to the female reproductive tract so that maximum number of eggs is fertilized. Although courtship and mating latencies were longer in the double inversion strain, by increasing copulation duration the males enhance their fitness. Even fecundity, viability, and fertility were higher in the double inversion strain than all others. The result obtained in the present study thus confirms the observation of earlier workers (Bostock, 1956; Singh and Chatterjee, 1986).

The 2LA inversion strain performed less than even the inversion free strain particularly with reference to fecundity and viability. Although inversions have an adaptive function, not all inversions are adaptive at all environments. Perhaps this is the reason for low performance of the inversion 2LA with respect to fertility and viability.

Acknowledgments: The authors are grateful to the Principal, Yuvaraja's College, Department of Zoology, University of Mysore, Mysore -570005 for providing facilities. Authors are also grateful to UGC financial support for Minor research project to Dr. S.C. Jayaramu.

References: Barker, J.S.F, 1981, [Proceeding of the 1979, Kioloa Conference] (Gibson, J.B., and J.G. Oakeshott, eds.). Australian National University: Canberra, pp. 161-184; Barker, J.S.F, and J.C. Mulley 1976, Evolution 30: 213-33; Bastock, M., 1956, Evolution 10: 421-439; Bock, I.R., and M.R. Wheeler 1972, Univ. Tex. Publ. 7213: 1-102; David, J.R., 1982, Biochem. Genet. 20: 747-761; Davis, B.J. 1964, Annals N.Y. Acad. Sci. 121: 404-427; Futch. D., 1966, Univ. Texas Publ. 6615: 79-120; Hegde, S.N., and M.S. Krishna 1997, Animal Behaviour 54: 419-426; Hegde, S.N., and N.B. Krishnamurthy 1976, Proc. Dunn. Dobzh. Symp. Genet. 36-42; Hegde, S.N., V. Vasudev, M.S. Krishna, and V. Shakunthala 1999, Entomon 24(2): 149-156; Hill, W.G., 1975, Theor. Popul. Biol. 8: 117-128; Johnson, F.M., 1971, Genetics 68: 75-95; Kesslller, S., 1968, Anim. Behav. 16: 485-490; Knibb, W.B., J.G Oakeshoff, S.R. Wilson 1987, Heredity 59: 95-104; Krimbas, C.B., and J.R. Powell 1993, Edited by C.B. Krimbas and J.R. Powell. C.R.C. Press. Boca Raton FL, pp.1-52; Langley, C.H., K. Ito, and R.A Voelker 1977, Genetics 86: 447-454; Markow, T.A., 1978, Nature, London 276: 821-822; Mettler, L.E., R.A. Voelker, and T. Mukai 1977, Genetics 87: 169-176; Parsons, P.A., 1965, Experientia 27: 478-485; Rajeshwari, P., and N.B. Krishnamurthy 1969, Indian Journal of Heredity 1: 143-147; Reddy, G.S., and N.B. Krishnamurthy 1974, Dros. Inf. Serv. 51: 136-137; Singh, B.N., 1985, Nucleus 28: 169-176; Singh, B.N., and S. Chatterjee 1986, Heredity 57: 75-78; Singh, B.N., and S. Chatterjee 1987, Genetica 73: 237-242; Singh, B.N., and S.R. Singh 1999, Curr. Sci. 77: 1200-1203; Sisodia, S., and B.N. Singh 2001, Curr. Sci. 80: 1444-1447; Sisodia, S., and B.N. Singh 2005, J. Genetics 84(2): 195-216; Smith, M.J., 1956, J. Genet. 54: 261-279; Spiess, E.B., 1970, In: *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky*. (Hecht, M.K., and W.C. Steere, eds.). Appleton-Century-Crofts. New York, pp- 315-379; Spieth, H.T, 1968, Evolutionary Biology 2: 157-191; Spieth, H.T., and J.M. Ringo 1983, In: *Genetics and Biology of* Drosophila, Vol. 3c. (Ashburner, M., H.L. Carson, and J.N. Thompson, jr., eds.). Academic Press, New York, pp 223-284; Zouros, E., and W. Johnson 1976, Canadian J. of Genetics and Cytology 1.

Inversion polymorphism, sexual behavior, fitness, and morphometric traits in *Drosophila ananassae*.

Jayaramu, S.C.*, and M. Prathibha. Department of Zoology, Yuvaraja's College, University of Mysore, Mysore -570005, Karnataka state, India. *Corresponding Author's E-mail: jayaramu21@gmail.com; prathibhajayaramu@gmail.com

Abstract

In the present study experimental stocks of *Drosophila ananassae* carrying 2LA, 3LA, 2LA+3LA inversions and a stock without any inversion were established from wild caught flies collected at Mysore, India. The mating activities (male courtship activities such as tapping, scissoring, vibration, circling, licking; activities of non-receptive females such as ignoring, extruding,