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Male age influence on mating activities of monomorphic and polymorphic strains of *Drosophila ananassae*.

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Introduction

Females of a species select males to derive either direct or indirect fitness benefits. Therefore, male success in mating depends on his ability to provide material benefits to mating female or genetic benefit to their offspring. Thus, females of a species use a variety of male phenotypes to select the potential mate (Anderson, 1994). Male age is one such trait used as reliable signal to determine male quality as has been shown in earlier studies of age based female mate choice experiments (Avent *et al.*, 2008; Beck and Powell, 2000). A series of verbal models (Trivers, 1972; Manning, 1985, 1989) predict that, given a choice, females should prefer older mates. As old males have proven survival ability, choosy females may gain indirect benefits from their choice of an old mate through the production of higher quality offspring. However, testing the effects of indirect benefit unequivocally requires exploration of the effects of female mating preferences on offspring survival and reproduction.

In species of *Drosophila* inversion karyotypes are known to influence on mating activity, mating advantage, mating speed, and female mate preference (Spiess and Langer, 1964a, b; Day and Butlin, 1987). It was also found that age based female mate preference is in a few species of

Drosophila (Avent *et al.*, 2008). These studies have found females of these species prefer to mate with older of the two competing males, and female mating with older male obtains indirect genetic benefits to their offspring. However, it is not known the role of inversion karyotypes on age based female mate preference.

Therefore, the present study has been undertaken in *D. ananassae*, a cosmopolitan domestic species, having a high degree of inversion polymorphism. The Indian natural populations of this species are genetically at the level of chromosomal polymorphism (Singh 1985a, b). The subterminal (alpha) inversion has become universally established in the species (Singh, 1970). Further it is known that behavioral properties are controlled by chromosomal variants. Therefore, in the present study a polymorphic strain has been established to rule out the role of inversion system in age based female mate preference. Although a number of adaptive functions have been found to be associated with inversion polymorphism, the association of mate choice, male age with inversion polymorphism has not been studied. Therefore, the present study was undertaken in *D. ananassae* to understand the relationship between male age, mate choice, and inversion polymorphism. So in *D. ananassae* we have used both monomorphic and polymorphic strains to study interrelation between male age, inversion system, and male reproductive success.

Materials and Methods

Experimental stock: Population without inversion (monomorphic population) and population with inversion (polymorphic population-2LA, 3LA, and 3RA inversion) of *D. ananassae* were established from progenies of 50 isofemale lines collected at semi domestic localities of Mysore, Karnataka, India (see more details in Prathibha, 2011). These culture bottles were maintained at $21 \pm 1^\circ\text{C}$ at a relative humidity of 70% using 12:12 L: D cycle. Virgin female and unmated males were isolated within 3 hrs of their eclosion and were aged individually in a vial containing wheat cream agar medium until they were used in the experiment.

There is a pericentric inversion in *D. ananassae* on the X or A element that converts the normally acrocentric X into a metacentric chromosome. A further remarkable karyotypic change can also be seen on Muller element F of *D. ananassae*. The F element that is normally a small, dot-like chromosome is a large metacentric that is equivalent in size to the X or A element. The large autosomes of *D. ananassae* are products of centromeric fusions between the B and C elements (symbolized as Muller element B_C for chromosome (3LA-3RA) and D_E elements 2LA (Stephen *et al.*, 2008).

Selection of male age classes: Before assigning male age classes we studied the longevity of male in monomorphic and polymorphic strains of *D. ananassae* by transferring individually unmated male into a vial containing wheat cream agar medium once in a week and maintained them in the same condition. This process was continued until their death and longevity was recorded. A total of 50 replicates were made for each of monomorphic and polymorphic strains, and mean longevity data showed 60 ± 2 days for monomorphic and 63 ± 2 days for polymorphic strain. Since mean longevity of *D. ananassae* ranges from 60-65 days we assigned days for young, middle, and old aged male as follows [Young age male (2-3 days), middle age male (24-25 days), and old age male (46-47 days)]. In addition to this, we also collected 5-6 days old virgin females from the respective stocks to use in the present experiment.

Mate choice tests: A female along with two competing males from different male age classes (young *v* middle age; young *v* old age; middle *v* old age; N =5 0 dyads per male pairing) were individually transferred into an Elens-Wattiaux mating chamber (1964). The effect of paint was

tested before commencing the experiment by painting one of the two young /middle/old age males and allowing them to mate. This pair was observed for 1 hr. There was no effect of the presence of paint on the probability of mating (all groups $P > 0.50$). When mating occurred, pairs in copulation were aspirated out from the mating chamber. Rejected male in female mate choice experiment was also transferred to new vial. A total 50 trials were made separately for each combination of female mate choice experiment. We also measured wing length of 50 selected and rejected males in each combination of the female mate choice experiment following the procedure of Hegde and Krishna (1997). Separate experiments were conducted for both monomorphic and polymorphic strains.

Evaluation of mating activities in monomorphic and polymorphic strains: We used unmated young, middle and old aged males and 5-6 days old virgin female of monomorphic and polymorphic strains (monomorphic male with monomorphic female; polymorphic male with polymorphic female) to study male age influence on male mating activities. A female along with a male (young/middle/old age) were individually transferred into an Elens-Wattiaux mating chamber and observed for 1hr. A pair unmated within 1 hr was discarded. We recorded mating latency (time between introduction of male and female together into mating chamber until initiation of copulation of each pair) and copulation duration (time between initiation of copulation to termination of copulation of each pair). We also quantified courtship acts such as tapping, scissoring, vibration, licking, circling, ignoring, extruding, and decamping following the procedure of Hegde and Krishna (1997). The behavior of male and female was recorded simultaneously but separately by two observers for 1 hr; the number of pairs mated was also recorded. Soon after copulation mated female was individually aspirated into a new vial containing wheat cream agar medium to check that insemination has occurred or not (by observing larval activity). Mated male was allowed to mate with second female (virgin 5-6 days old). If mating occurred with second female, we allowed the pair to complete copulation and checked for insemination as above. This process was continued and the number of females inseminated by each male in 1 hr was recorded as male mating ability.

Statistical analysis: A total of 50 trials were used separately for each of the three male age classes. Chi-square analysis was carried out on data of female mate choice experiment and paired 't' test on wing length of selected and rejected males in female mate choice experiment. One-way ANOVA followed by Tukey's Honest *post hoc* test (Tukey's test) was carried out on data of mating activities, courtship activities using SPSS 10.0 Programme. In addition Bonferroni correction factor was applied on courtship activity data (tapping, scissoring, vibration, licking, ignoring, extruding, and decamping).

Results and Discussion

Mate choice tests: In both monomorphic and polymorphic strains females of *D. ananassae* generally chose to mate with the older of the two competing males of different age classes. Success of old males in crosses involving young and old aged males was 70% in monomorphic strain ($\chi^2 = 8.00$ df = 1; $P < 0.05$; N = 50) and 68% in polymorphic strain ($\chi^2 = 20.48$ df = 1; $P < 0.05$; N = 50). Success of middle aged males involving young and middle aged males was 72% in monomorphic strain ($\chi^2 = 6.48$ df = 1; $P < 0.05$; N = 50) and 73% in polymorphic strain ($\chi^2 = 9.68$ df = 1; $P < 0.05$; N = 50). Old males success in crosses involving middle and old aged males was 64% in monomorphic strain ($\chi^2 = 3.92$ df = 1; $P < 0.05$; N = 50) and 66% in polymorphic strain ($\chi^2 = 5.12$; df = 1; $P < 0.05$; N = 50).

Mean wing length of rejected males was slightly greater than that of mean wing length of selected males in all the combinations of female mate choice experiment in monomorphic and polymorphic strains studied (Table 1). Paired 't' test carried out on mean wing length data of

selected and rejected males showed insignificant variation in both monomorphic and polymorphic strains.

Table 1. Mean wing length (in mm) of selected and rejected males of monomorphic and polymorphic strains of *D. ananassae* in female choice experiment (Values are mean \pm SE).

Strains	Crosses		Wing length (in mm)		t- value
	Female	Males	Selected male	Rejected male	
Monomorphic	5-6 days	Young, old	1.701 \pm .006	1.710 \pm .005	1.79 ^{NS}
Polymorphic		Young, old	1.738 \pm .006	1.744 \pm .007	0.85 ^{NS}
Monomorphic	5-6 days	Middle, old	1.716 \pm .004	1.718 \pm .005	0.74 ^{NS}
Polymorphic		Middle, old	1.751 \pm .016	1.763 \pm .020	0.63 ^{NS}
Monomorphic	5-6 days	Young, middle	1.719 \pm .006	1.721 \pm .006	1.40 ^{NS}
Polymorphic		Young, middle	1.767 \pm .015	1.772 \pm .014	0.36 ^{NS}

NS- Non significant; df – 49.

Table 2. Male age influence on male courtship and mating activities in monomorphic and polymorphic strains of *D. ananassae* (Values are Mean \pm SE).

Parameters	Strains	Male			F-values (df-2,147, 149)
		Young (2-3days)	Middle (24-25 days)	Old (46-47days)	
Mating latency (in min)	Mono	24.68 \pm .79 ^a	19.90 \pm .64 ^b	14.56 \pm .51 ^c	58.87**
	Poly	18.86 \pm .68 ^x	13.74 \pm .52 ^y	10.20 \pm .37 ^z	64.27**
Tapping (in no)	Mono	8.92 \pm .21 ^a	10.88 \pm .28 ^b	11.86 \pm .29 ^c	30.67**
	Poly	9.84 \pm .34 ^x	11.56 \pm .34 ^y	12.88 \pm .37 ^z	18.43**
Scissoring (in no)	Mono	9.96 \pm .35 ^a	11.08 \pm .31 ^b	12.08 \pm .36 ^c	9.44**
	Poly	11.56 \pm .4 ^x	12.14 \pm .38 ^y	13.12 \pm .42 ^z	10.12**
Vibration (in no)	Mono	8.50 \pm .35 ^a	9.04 \pm .39 ^a	11.00 \pm .47 ^b	10.37**
	Poly	9.02 \pm .41 ^x	10.34 \pm .56 ^x	12.60 \pm .39 ^y	15.13**
Circling (in no)	Mono	3.40 \pm .15 ^a	3.98 \pm .14 ^b	4.78 \pm .15 ^c	21.06**
	Poly	3.76 \pm .18 ^x	5.52 \pm .20 ^y	7.08 \pm .33 ^z	43.02**
Licking (in no)	Mono	3.08 \pm .19 ^a	4.00 \pm .21 ^b	4.66 \pm .16 ^c	16.83**
	Poly	3.74 \pm .26 ^x	4.36 \pm .21 ^y	5.24 \pm .17 ^z	11.65**
Ignoring (in no)	Mono	5.54 \pm .24 ^a	4.32 \pm .16 ^b	3.54 \pm .20 ^c	26.14**
	Poly	5.04 \pm .25 ^x	3.96 \pm .17 ^y	2.98 \pm .16 ^z	25.94**
Extruding (in no)	Mono	4.94 \pm .19 ^a	3.50 \pm .14 ^b	2.74 \pm .13 ^c	47.56**
	Poly	4.42 \pm .20 ^x	3.24 \pm .13 ^y	2.32 \pm .12 ^z	44.22**
Decamping (in no)	Mono	3.80 \pm .16 ^a	3.12 \pm .17 ^b	2.48 \pm .11 ^c	18.43**
	Poly	3.46 \pm .15 ^x	2.92 \pm .16 ^y	2.12 \pm .12 ^z	19.95**
Copulation duration (in min)	Mono	3.14 \pm .03 ^a	3.64 \pm .04 ^b	4.04 \pm .04 ^c	87.02**
	Poly	3.74 \pm .05 ^x	4.15 \pm .04 ^y	4.35 \pm .05 ^z	37.40**
Male mating ability (in no)	Mono	1.24 \pm .06 ^a	1.46 \pm .07 ^b	1.72 \pm .07 ^c	12.62**
	Poly	1.66 \pm .09 ^x	1.92 \pm .08 ^y	2.52 \pm .07 ^z	27.82**

**P < 0.001; Note: 1) Different letter (a, b, c for Monomorphic strain; x, y, z for polymorphic strain) in superscript in each row indicates significant by Tukey's test. 2) Mono= Monomorphic strain and Poly= polymorphic strain.

Mating activities: Table 2 shows mean values of courtship and mating activities data of both monomorphic and polymorphic strains. It was noticed that old aged male had lowest time for mating,

copulated longer, performed greater male courtship activities (tapping, scissoring, vibration, licking, circling), and inseminated more females than those of middle aged and young males. Female showed least rejection responses (ignoring, extruding, and decamping) to old aged males, while she showed highest rejection responses to young aged males. One-way ANOVA followed by Tukey's test carried out on mean mating latency, copulation duration, courtship activities, and male mating ability showed significant variation in all the above characters between male age classes, in both monomorphic and polymorphic strains (Table 2). Tukey's test showed that in both monomorphic and polymorphic strains old males had significantly less time for mating, copulation longer, and showed greater mating activities than middle aged and young males. However, wing vibration behavior of young and middle aged males was found to be insignificantly less than old males by Tukey's *post hoc* test. Similarly, middle aged males had significantly less time for mating latency, copulated longer, and showed greater mating activities compared to young males. In turn females significantly showed less rejection behavior to old males compared to middle aged and young males. Polymorphic strains showed significantly greater courtship, mating activities compared to monomorphic strain. In addition to this, principal component analysis has been carried out on courtship activity data Table 3 and Figure 1 (A to D). It was noticed that tapping, scissoring, vibration, and circling were known to influence significantly on male mating success in both monomorphic and polymorphic strains. In turn female rejection responses such as ignoring and extruding have significant influence on the mating success. This result was found to be similar both in monomorphic and polymorphic strains.

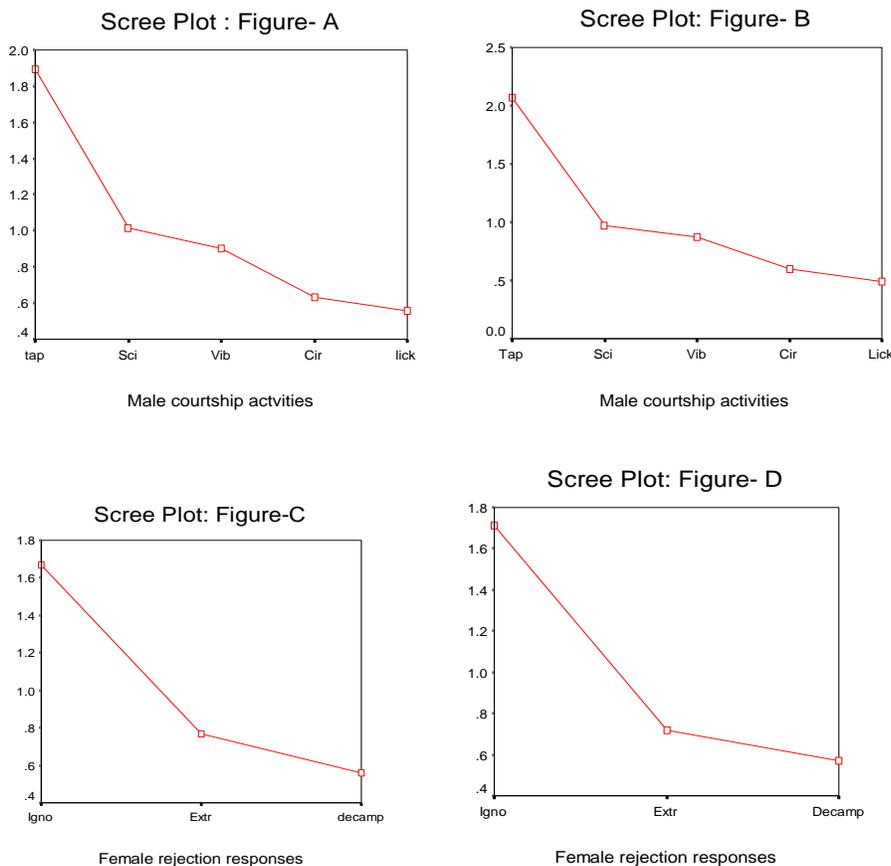


Figure 1. Scree plot of principle component analysis (for male courtship activities: A-Mono-morphic, B- polymorphic; female rejection responses: C-Mono-morphic, D- polymorphic strains) of *D. ananassae*.

Females of *Drosophila* are able to discriminate males on the basis of size and she preferred larger males more frequently over small males (Patridge *et al.*, 1987; Santos *et al.*,

1992; Hegde and Krishna, 1997; Krishna and Hegde, 2003). As more and more studies have been made, correlation between male size and male mating success was not found to be strong as thought previously (Markow *et al.*, 1996). Apart from male size, male age is another possible cue for female

Table 3. Principle component analysis for male courtship activities and female rejection responses in monomorphic and polymorphic strains of *D. ananassae*.

Male courtship activities		Initial Eigen values			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
		Total	% of variance	Cumulative %	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %
Monomorphic strain	Tapping	1.895	37.892	37.892	1.895	37.892	37.892	1.555	31.093	31.093
	Scissoring	1.018	20.350	58.243	1.018	20.350	58.243	1.357	27.150	58.243
	Vibration	0.903	18.055	76.298						
	Circling	0.630	12.598	88.895						
	Licking	0.555	11.105	100.000						
Polymorphic strain	Tapping	2.070	41.401	41.401	2.070	41.401	41.401			
	Scissoring	0.966	19.326	60.727						
	Vibration	0.873	17.455	78.182						
	Circling	0.602	12.049	90.231						
	Licking	0.488	9.769	100.000						
Female rejection responses										
Monomorphic strain	Ignoring	1.670	55.681	55.681	1.670	55.681	55.681			
	Extruding	0.770	25.664	81.345						
	Decamping	0.560	18.655	100.000						
Polymorphic strain	Ignoring	1.710	56.989	56.989	1.710	56.989	56.989			
	Extruding	0.719	23.977	80.966						
	Decamping	0.571	19.034	100.000						

Extraction Method: Principal Component Analysis

preference for male character. In the present study in both monomorphic and polymorphic strains of *D. ananassae* we found that females of *D. ananassae* can discriminate males on the basis of male age, and she preferred old males more frequently than young or middle aged males. This confirms the earlier studies of female discrimination for male age classes in *D. melanogaster* and *D. simulans* (Moulin *et al.*, 2001), in *D. pseudoobscura* (Avent *et al.*, 2008), and in *D. bipunctata* (Somashekar and Krishna, 2011). They found that in these species females preferred old males more than young. These results are also consistent with some previous observations in other insects and birds (Zuk, 1988; Conner, 1989; Hassalquist *et al.*, 1996) and also with the theoretical models of good gene hypothesis (Kokko, 1997, 1998) suggesting that female preference for old aged male can be an evolutionary stable strategy (Avent *et al.*, 2008). In a few of the above studies male age used in their studies did not match with their longevity (Moulin *et al.*, 2001).

In studies of female mate choice it is common that in addition to female preference, it also involves male-male competition (Avent *et al.*, 2008). Therefore, it was difficult to say observed mating success resulted due to female preference or the result of male-male competition. However, in studies of female choice it was suggested that male-male competition can reinforce female mate preferences rather than operating in an antagonistic fashion (Moore and Moore, 1999).

Insignificant variation was also found in mean wing length of selected and rejected males and even in some combination mean wing length of rejected males were slightly longer than that of selected males but showed insignificant (Table 1). This suggests that observed greater mating success of old aged males was not due to difference in the mean wing length between young, middle and old aged males. Instead it could be attributed to male age itself.

Rearing condition provided for young, middle, and old aged males in the experiment were the same and all these males were unmated; therefore, the observed greater mating success of old aged male cannot be attributed to difference in the rearing condition male experience and male mating

history as found in some previous experiments in insects (Svetec and Ferveur, 2005; Jones and Elgar, 2004).

Young, middle and old aged males of *D. ananassae* used here were fully mature and all show courtship activities. Males below 2nd day were immature; they do not show any courtship activities and males above 46-47 day started showing decline in courtship activities. Therefore, the observed lesser mating success of young or middle aged males may not be attributed to young and middle aged males being immature.

Another potential factor known to influence male mating success in *Drosophila* is male activities and female receptivity during courtship (Bastock, 1956; Hegde and Krishna, 1997). In our study in both monomorphic and polymorphic strains old aged male mated faster (as the time is reverse of the speed), copulated longer, and performed greater courtship activities than young or middle aged males (Table 2). Through these activities old aged male convinced the female faster and had greater mating success, because through these courtship acts male communicates with female through visual, chemical, tactile, and auditory stimuli. As a result he increases the female receptivity (Speith, 1966; Hegde and Krishna, 1997; Tompkin *et al.*, 1982). This confirms the earlier studies of courtship in different species of *Drosophila* suggesting that flies which show greater activities during courtship have greater mating success than males which show less activities (Hegde and Krishna, 1997). Females of *D. ananassae* showed less rejection activities, *i.e.*, extruding, decamping, ignoring to old aged males compared to young or middle aged males (Table 2). This suggests influence of male age on female receptivity. This confirms earlier studies of *Drosophila* where females which show less rejection response, have greater receptivity, and have greater mating success than the females which show greater rejection to courting males (Hegde and Krishna, 1997). Studies of sexual behavior in *Drosophila* suggest that courtship activity of male and female culminates in copulation (Spiess, 1970). In our study we noticed that old aged males copulated longer compared to young or middle aged males. This suggests male age influence on copulation duration. This supports the work of Avent *et al.* (2008) who while working in *D. pseudoobscura* has also found longer copulation duration of old age male. It is not known whether the delayed mating could be the reason for older male to copulate longer or not. A strong theoretical reason to expect greater duration of copulation of old age male was that old males have not encountered females for many days to be investigating more resources in the first female he encounters (Wedell *et al.*, 2002) or old age males have lower residual reproduction value and may increase their ejaculate investment per mating with increasing age (Roff, 1992). Also, old males may have accumulated a larger quantity of ejaculate (Sperm and Seminal fluids) that takes a longer time to transfer to the females (Jones *et al.*, 2007). In *D. pseudoobscura* it was found that males kept as virgins for 14 days had high ejaculate quantities (Avent *et al.*, 2008). This suggests that sperm quantity may increase with increasing male age.

The primary function of mating is the transfer of sperm to females, since each mating offers an opportunity for males to produce offspring. Males can generally increase their fitness by mating with many mates, and high mating rates are thus typically associated with high male reproductive success. In our study in both monomorphic and polymorphic strains, old age males had inseminated a greater number of females in a given unit of time than young or middle aged males (Table 2). This suggests that male age has significant influence on male mating ability and old age male had greater male fitness than young male. This supports the earlier studies of male flies which inseminate greater number of females have greater fitness than male flies which inseminate less number of females (Thornhill and Alcock, 1983; Krishna and Hegde, 1997).

In our study we also found that polymorphic strain had greater mating activities over monomorphic strain (Singh and Chatterjee, 1988; Singh, 1989; Singh and Som, 2001).

Thus these studies in *D. ananassae* suggests that females of *D. ananassae* discriminate males on the basis of age and older males had greater reproductive success over young or middle age males, which is found to be independent from influence of inversion system.

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Male age effects on fitness are independent of inversion system in *Drosophila ananassae* (Diptera: Drosophilidae).

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