



Male age effect on mating success is independent of inversion system in *Drosophila ananassae*.

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Abstract

Male age influence on mating success, courtship, and mating activities has been studied in monomorphic (inversion free) and polymorphic (with inversion) strains of *Drosophila ananassae*. It was noticed that in both monomorphic and polymorphic strains, females of *D. ananassae* were able to discriminate males on the basis of male age and preferred to mate with old aged males more frequently than young or middle aged males using female choice experiments. Old aged males significantly mated faster, performed greater courtship activities, copulated longer than females mated to young or middle aged males. Thus, in *D. ananassae* male age influence on mating success is independent of inversion system. Key Words: *Drosophila ananassae*, monomorphic, polymorphic, male age, female preference, courtship activities.

Introduction

In the field of behavioral biology from the time of Darwin females of a species exercise their choice in mating to obtain potential male was shown to exist in many taxa (Andersson, 1994). Females use number of male traits to select male such as size, mating care, courtship song, pigmentation, and so forth (Somashekar *et al.*, 2011). In recent years it was shown that females of a species could also use male age as a cue to select male in the mating to derive either direct or indirect benefits (Trivers, 1972; Hansen and Price, 1995; Kokko and Lindstrom, 1996). Different models have been proposed for female preference to male age in different organisms. Good gene model is one such model which predicts that females of a species should select the old age male to obtain indirect genetics benefits. This model is based on the assumption that old males have proven their survival ability since only the fittest males should be able to survive to old age suggesting they have higher genetic quality. Therefore, females mating with such males could obtain better offspring qualities than the females mated with young age males (Brooks and Kemp, 2001). Some empirical evidence has also been found for female preference for old male in a few taxa (Wedell *et al.*, 2002; Simmons and Zuk, 1997; Simmons, 1995; Manning, 1989). In contrast to this the others are of the opinion that the female should select young males as they have accumulated fewer germ line mutations (Crow, 1993), that the presence of negative genetic correlations between traits results in trade-offs between early and late fitness components (Cordts and Partridge, 1996) or in long lived organisms, and that offspring born to younger parents are better adapted to current environmental conditions, because their parents were exposed to recent selection (Hansen and Price, 1995). When factors such as the allocation of resources to sexual traits, variations in male condition and age specific survival probability were included, the models showed that preferences for older males could evolve (Kokko, 1997; 1998; Hansen and Price, 1999; Beck and Powell, 2000; Beck and Promislow, 2007; Beck *et al.*, 2002). However these models also predicted that preferences for younger males are equally possible, depending upon the conditions specified. The difference in conclusions of these models is a probable result of their contrary approaches towards the change in physiological state of males with age and the existence of life history tradeoffs. Unless more species and genera are involved, it is difficult to understand the concept. Hence more studies are needed in this regard. To test these, model species of *Drosophila* as they do not show parental care is more suitable.

D. ananassae has been selected as the experimental model in the present investigation because of its following characteristics. It is a cosmopolitan domestic species belonging to *melanogaster* group of *ananassae* sub group and *ananassae* species complex (Bock and Wheeler, 1972). This species occupies a unique status in the whole of the genus *Drosophila* due to certain peculiarities in its genetical behavior (Singh, 1985a, b). Presence of male crossing over, high level of inversion polymorphism and high mutability are the

features which make it useful for certain genetic studies. Therefore, the present study has been undertaken in *D. ananassae* to study the role of inversion system in male age effect of mating activity.

Materials and Methods

Monomorphic (Inversion free) and polymorphic (with inversion) strains of *D. ananassae* that were established from out-bred populations collected at semi domestic localities of Mysore, Karnataka, India have been used to study male age effects on mating success. To study polytene chromosomes and to screen for the presence of inversions, the larvae were dissected in 0.7% sodium chloride solution. These salivary glands were fixed in 1N HCl for five minutes. The stained glands were individually placed on slides with two drops of 45% acetic acid. Then salivary glands were squashed by placing a clean cover glass and by applying uniform pressure. This achieves uniform spreading of the chromosomes. After squashing, edges of the cover slip were sealed with paraffin lanolin mixture. The observation of slides were done under Leitz Ortholux II scientific and clinical microscope both at low (10×) and high (45×) magnification. If inversion loop is present in the larvae then the mother of those larvae was treated as polymorphic. If there is no inversion loop in the larvae then the mother of those larvae was treated as monomorphic. Presence or absence of inversions was checked for 5 generations. Like this polymorphic and monomorphic strains were established. These experimental stocks were maintained at $21 \pm 1^\circ\text{C}$ at relative humidity of 70% using 12:12 L:D cycle. At the 5th generation after testing the inversion, virgin females and bachelor males were isolated within 3 hr of their eclosion separately from monomorphic and polymorphic strains and aged as required and cultured using the same laboratory condition until they were used in the experiments.

Selection of male age classes

Before assigning male age classes, we studied the longevity of males in monomorphic and polymorphic strains of *D. ananassae* by transferring an individually unmated male into a vial containing wheat cream agar medium once in a week and maintaining 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 $60 \pm$ 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 (2-3days), middle age male (24-25 days), and old age male (46-47days)]. In addition to this, we also collected 5-6 days old virgin females from the respective stocks and these were used in the present experiment.

Male age influence on male mating success in monomorphic and polymorphic strains

Five-six day old virgin females and unmated young, middle, old aged males of monomorphic and polymorphic strains were used to study male age influence on male mating success using female mate choice experiment. A female along with two males of different male age classes were individually transferred into an Elens-Wattiaux mating chamber (Elens and Wattiaux, 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. Between young age males in 24 out of 50 trials, males painted were mated and in the remaining 26 out of 50 trials males that were not painted were mated ($\chi^2 = 0.08$, $\text{df} = 1$; $P > 0.05$), for middle age males in 23 out of 50 trials, males painted were mated and in the remaining 27 out of 50 trials unpainted males were mated ($\chi^2 = 0.32$, $\text{df} = 1$; $P > 0.05$), and for old age males in 24 out of 50 trials, male painted were mated while in the remaining 26 out of 50 trials, males not painted were mated ($\chi^2 = 0.08$, $\text{df} = 1$; $P > 0.05$). Thus, these results indicated that painting of one of the competing males in female mate choice experiments did not have an effect on the performance of the flies). Observation was made for 1 hr. When mating occurred, pairs in copulation were aspirated out from the mating chamber. Rejected males in the female mate choice experiment were also transferred to new vials. Separate experiments were conducted for both monomorphic and polymorphic strains. A total of 50 trials were made separately for each combination of female mate choice experiment, and Chi-square analysis was applied to the data of female mate choice experiments. 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), and Paired 't' test was applied to the data.

Male age influence on mating activities in monomorphic and polymorphic strains

We used unmated young, middle, and old aged males and 5-6 days old virgin females of monomorphic and polymorphic strains 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 1 hr. Pair unmated within 1 hr were 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 males and females was recorded simultaneously but separately by two observers for 1 hr; the number of pairs mated was also recorded.

A total of 50 trials were used separately for each of the three male age classes. Two 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. Experiments were done separately for both monomorphic and polymorphic strains.

Results

Male age influence on male mating success

In both monomorphic and polymorphic strains, females of *D. ananassae* generally chose to mate older of the 2 competing males of different age classes (Figures 1a, 1b, and 1c; Tables 1a, 1b, and 1c). In monomorphic strain: in 70% of cases, older males were successful in crosses involving young and old aged males ($\chi^2 = 8.00$, $df = 1$; $P < 0.05$; $N = 50$); in 68% of cases middle aged males were successful in crosses involving young and middle aged males ($\chi^2 = 6.48$, $df = 1$; $P < 0.05$; $N = 50$). In 64% of cases, old aged males were successful in crosses involving middle and old aged males ($\chi^2 = 3.92$, $df = 1$; $P < 0.05$; $N = 50$). While in polymorphic strain: In 82% of cases, older males were successful in crosses involving young and old aged males ($\chi^2 = 20.48$, $df = 1$; $P < 0.05$; $N = 50$); in 72% of cases middle aged males were successful in crosses involving young and middle aged males ($\chi^2 = 9.68$, $df = 1$; $P < 0.05$; $N = 50$). In 66% of cases, old aged males were successful in crosses involving middle and old aged males ($\chi^2 = 5.12$, $df = 1$; $P < 0.05$; $N = 50$).

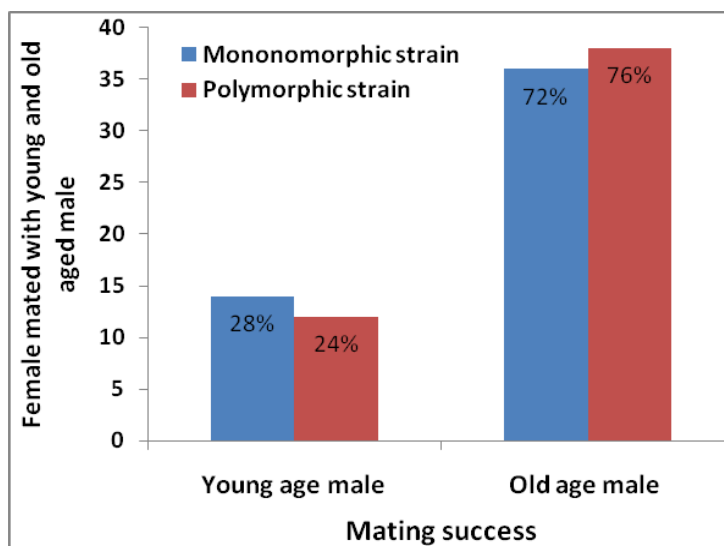


Figure 1a. Female preference for young and old aged males in monomorphic and polymorphic strains of *D. ananassae*.

Table 1a. Female preference for young and old aged males in monomorphic and polymorphic strains of *D. ananassae*.

Strains	Female	Males	Female mated with YAM	Female mated with OAM	χ^2 - Value
Monomorphic	5-6 days	YAM + OAM	14 (28%)	36 (72%)	9.68*
Polymorphic	5-6 days	YAM + OAM	12 (24%)	38 (76%)	13.52*

*Significant at 0.01 level; YAM-Young age male; OAM- Old age male

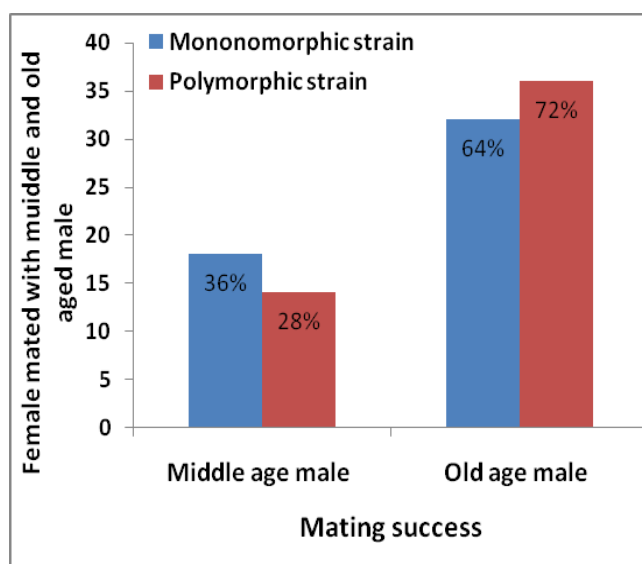


Figure 1b. Female preference for middle and old aged males in monomorphic and polymorphic strains of *D. ananassae*.

Table 1b. Female preference for middle and old aged males in monomorphic and polymorphic strains of *D. ananassae*.

Strains	Female	Males	Female mated with MAM	Female mated with OAM	χ^2 - Value
Monomorphic	5-6 days	MAM + OAM	18 (36%)	32 (64%)	3.92*
Polymorphic	5-6 days	MAM + OAM	14 (28%)	36 (72%)	9.68**

* Significant at 0.05 level, **Significant at 0.01 level; MAM- Middle age male; OAM- Old age male.

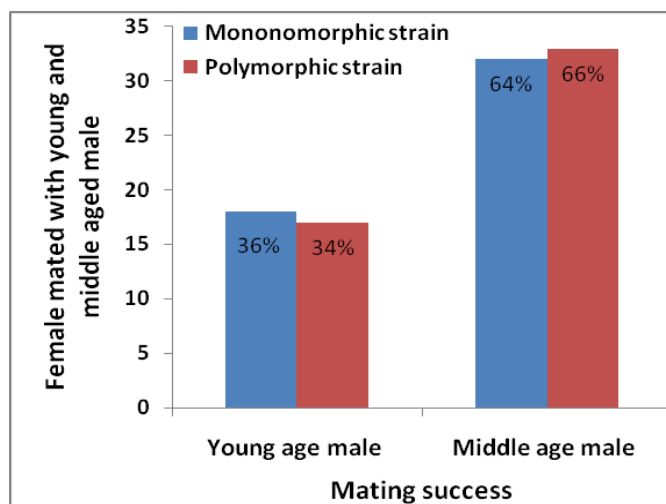


Figure 1c. Female preference for young and middle aged males in monomorphic and polymorphic strains of *D. ananassae*.

Table 1c. Female preference for young and middle aged males in monomorphic and polymorphic strains of *D. ananassae*.

Strains	Female	Males	Female mated with YAM	Female mated with MAM	χ^2 - Value
Monomorphic	5-6 days	YAM + MAM	18 (36%)	32 (64%)	3.92*
Polymorphic	5-6 days	YAM + MAM	17 (34%)	33 (66%)	5.12*

* Significant at 0.05 level; YAM-Young age male; MAM- Middle age male

Male age influence on selected and rejected male

Mean wing length of rejected males was slightly greater than that of mean wing length of selected males in all the combinations of monomorphic and polymorphic strains studied (Table 2). 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 2. 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	YAM + OAM	1.701 \pm .006	1.710 \pm .005	1.79 ^{NS}
Polymorphic		YAM + OAM	1.738 \pm .006	1.744 \pm .007	0.85 ^{NS}
Monomorphic	5-6 days	MAM + OAM	1.716 \pm .004	1.718 \pm .005	0.74 ^{NS}
Polymorphic		MAM + OAM	1.751 \pm .016	1.763 \pm .020	0.63 ^{NS}
Monomorphic	5-6 days	YAM + MAM	1.719 \pm .006	1.721 \pm .006	1.40 ^{NS}
Polymorphic		YAM + MAM	1.767 \pm .015	1.772 \pm .014	0.36 ^{NS}

NS- Non significant; df -49.

Male age influence on courtship and mating activities

Table 3 shows mean values of courtship and mating data of both monomorphic and polymorphic strains. It was noticed that old aged male had the lowest mating latency, copulated longer, and performed greater male courtship activities (tapping, scissoring, vibration, licking, circling), while the reverse trend was found in the above characters in young aged males. Females showed least rejection responses (ignoring, extruding, and decamping) to old aged males, while she showed greater rejection responses to young aged males. Two Way ANOVA followed by Tukey's test carried out on mean mating latency, copulation duration, courtship activities data using SPSS 10.0 programme showed significant variation in all the above characters among males of different age classes, between monomorphic and polymorphic strains, and also interaction between age and strains (Table 3). Tukey's test showed that in both monomorphic and polymorphic strains old aged males had significantly lesser mating latency, greater copulation duration, mating activities than young or middle aged males except vibration. Vibration by young and middle aged males was found to be insignificant by Tukey's test. Similarly, middle aged males had significantly greater mating latency, copulation duration, mating activities compared to young aged males. Females showed significantly greater rejection responses to young aged males compared to old and middle aged males. Polymorphic strains showed significantly greater courtship, mating characters compared to monomorphic strains.

Table 3. Male age influence on male courtship and mating activities in monomorphic and polymorphic strains of *D. ananassae* (Values are Mean \pm SE).

Parameters	Strains	Males			F-values		
		Young (2-3days)	Middle (24-25days)	Old (46-47days)	F1 = between strains (df-1, 294)	F2 = between ages (df-2, 294)	F3 = between strains & ages (df-6, 294)
Mating latency	Mono	24.68 \pm .79a	19.90 \pm .64b	14.56 \pm .51c	121.87**	120.86**	1.25NS
	Poly	18.86 \pm .68a	13.74 \pm .52b	10.20 \pm .37c			
Tapping	Mono	8.92 \pm .21a	10.88 \pm .28b	11.86 \pm .29c	11.49**	45.70**	.15NS
	Poly	9.84 \pm .34a	11.56 \pm .34	12.88 \pm .37c			
Scissoring	Mono	9.96 \pm .35a	11.08 \pm .31b	12.08 \pm .36c	8.55**	19.43**	.23NS
	Poly	11.56 \pm .4a	12.14 \pm .38b	13.12 \pm .42c			
Vibration	Mono	8.50 \pm .35a	9.04 \pm .39a	11.00 \pm .47b	10.16**	25.30**	.81NS
	Poly	9.02 \pm .41a	10.34 \pm .56a	12.60 \pm .39b			
Circling	Mono	3.40 \pm .15a	3.98 \pm .14b	4.78 \pm .15c	67.65**	63.53**	10.99**
	Poly	3.76 \pm .18a	5.52 \pm .20b	7.08 \pm .33c			
Licking	Mono	3.08 \pm .19a	4.00 \pm .21b	4.66 \pm .16c	9.90**	27.53**	.28NS
	Poly	3.74 \pm .26a	4.36 \pm .21b	5.24 \pm .17c			
Ignoring	Mono	5.54 \pm .24a	4.32 \pm .16 b	3.54 \pm .20c	7.32*	47.75**	.12NS
	Poly	5.04 \pm .25a	3.96 \pm .17 b	2.98 \pm .16c			
Extruding	Mono	4.94 \pm .19a	3.50 \pm .14b	2.74 \pm .13c	9.35**	91.52**	.33NS
	Poly	4.42 \pm .20a	3.24 \pm .13b	2.32 \pm .12c			
Decamping	Mono	3.80 \pm .16a	3.12 \pm .17b	2.48 \pm .11c	5.81*	38.19**	.16NS
	Poly	3.46 \pm .15a	2.92 \pm .16b	2.12 \pm .12c			
Copulation duration	Mono	3.41 \pm .03a	3.64 \pm .04b	4.04 \pm .04c	96.33**	84.54**	2.87NS
	Poly	3.74 \pm .05a	4.15 \pm .04b	4.35 \pm .05c			

*P < 0.05; **P < 0.001; NS-insignificant.

Notes: 1) Different letter in superscript in each row indicates significant by Tukey's test. 2) Mating latency and copulation duration are measured in minutes while other parameters are measured in numbers.

Discussion

In *Drosophila ananassae* it was noticed from mating success that in both monomorphic and polymorphic strains, the female was able to discriminate males on the basis of male age and she preferred to mate more frequently with old aged males than with young or middle aged males (Figures 1a, 1b, and 1c; Tables 1a, 1b, and 1c). This suggests that female preference for old age is independent of inversion system. Our study also supports female preference for old age male studies in *D. melanogaster* and *D. simulans* (Moulin *et al.*, 2001) and in *D. pseudoobscura* (Avent *et al.*, 2008). That suggests that females of these species were able to discriminate males on male age classes and she mates with old aged males more frequently over young aged males. This result is also consistent with some previous observations in other insects and birds (Singh and Som, 2001; Conner, 1989; Hasselquist, 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 evolutionarily stable strategy (Avent *et al.*, 2008). In contrast to this, studies of Hansen and Price (1995) and Price and Hansen (1998) in *D. melanogaster* have argued that females prefer to mate with young males more frequently than old aged males. However, empirical evidence in this regard is absent in *Drosophila*.

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 whether 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).

In studies of *Drosophila* it was found that male size is important of his success in mating (Partridge *et al.*, 1987; Santos *et al.*, 1992; Hegde and Krishna, 1997). 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 (Table 2). In the present study wing lengths of selected and rejected males were also measured. 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 males cannot be attributed to differences in the rearing condition, male experience, and male mating history as found in some previous experiments in insects (Jones and Elgar, 2004; Svetec and Ferveur, 2005).

Young, middle, and old aged males of *D. ananassae* used here were fully mature and all showed courtship activities. Males below 2nd day were immature; they do not show any courtship activities and males above 46-47 days 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.

In *Drosophila* the success of males in mating also depends on mating activities performed to convince the female (Bastock, 1956; Hegde and Krishna, 1997). In our study in both monomorphic and polymorphic strains, old aged males mated faster (as the time is reverse of the speed), copulated longer, and performed greater courtship activities than young or middle aged males (Table 3). Through these activities old aged males convinced the female faster and had greater mating success because through these courtship acts the male communicates to the female through visual, chemical, tactile, and auditory stimuli. As a result he increases the female receptivity (Speith, 1966; Tompkins *et al.*, 1982; Hegde and Krishna, 1997). 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 3). This suggests influence of male age on female receptivity. This confirms earlier studies of *Drosophila* where females which show less rejection responses, 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 a 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 males. It is not known whether the delayed mating could be the reason for older male to copulate longer or not. There is a strong theoretical reason to expect for greater duration of copulation of old age males was that old males have not encountered females for many days to be investing 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 that were 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.

This confirms the earlier studies of greater mating activities of polymorphic strain over monomorphic strain (Dobzhansky and Levene, 1951; Jayaramu, 2009). Thus, in *D. ananassae* male age influence on mating success is independent of inversion system.

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Greater fitness of middle aged females in monomorphic and polymorphic strains of *Drosophila ananassae*.

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Abstract

Monomorphic (inversion free) and polymorphic (with inversion) strains of *Drosophila ananassae* established from out-bred population collected at Mysore have been used to study female age influence on fecundity, fertility, and ovariole number. It was noticed that polymorphic strains had greater fecundity, fertility, and ovariole number than monomorphic strains. It was also noticed that in both monomorphic and polymorphic strains middle aged females had significantly greater fecundity, fertility, ovariole number than young or old aged females. Thus, in *D. ananassae* middle aged females had higher reproductive fitness than young or old aged females, which is independent of inversion system. Key Words: *Drosophila ananassae*, female age, male mate preference, ovariole number, monomorphic and polymorphic.

Introduction

Male mate choice is expected in systems where males allocate valuable resources to parental investment, in response to variation in female quality or where the costs of mate search and/or assessment are