determined by different loci at different ages, with no genetic correlation between early and late age fecundities (Leips *et al*., 2006). In our study we also found that polymorphic strains had greater reproductive success over monomorphic strains (Singh, 1989; Singh and Chatterjee, 1988; Singh and Som, 2001). This confirms the earlier studies of greater fitness of polymorphic strains over monomorphic strains (Dobzhansky and Levene, 1951; Jayaramu, 2009). Thus, these studies in *D. ananassae* suggest 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.

Acknowledgment: The authors are grateful to UGC for sanctioning Teacher Fellowship and also grateful to the Professor and Chairman, Department of Studies in Zoology, and also grateful to Principal, Yuvaraja's College, Mysore, University of Mysore, for providing facilities.

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Reproductive advantage 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 populations collected at Mysore has been used to study female age influence on mating success, mating latency, courtship activities, copulation duration, and female wing length. It was noticed that polymorphic strains had greater mating success, mated faster, performed greater courtship activities, and copulated longer than monomorphic strains. It was also noticed that in both monomorphic and polymorphic strains middle aged females had significantly greater mating success, mated faster than young or old aged females. Males showed significantly greater intensities of courtship activities, *i.e.*, tapping, scissoring, vibration, circling, licking to middle aged females compared to young or old aged females, copulated longer over young or old aged females. Middle aged females showed significantly less rejection responses, *i.e.*, ignoring, extruding, decamping to male compared to young or old aged females. However, insignificant variation was found in female wing length among females of different age classes. Thus, in *D. ananassae* middle aged females had reproductive advantage than young or old aged females, which is independent of inversion system. Key Words: *Drosophila ananassae,* female age, male mate preference, wing length, monomorphic and polymorphic.

Introduction

Most compelling studies on sexual selection have largely concentrated on females, as they are often the selective sex that chooses from amongst males (reviewed by Milinski, 2001). Now it is becoming increasingly apparent that in many species males, nevertheless, have a high cost of reproduction (mating) due to costs arising from factors such as energetically expensive courtship displays (Jones and Hunter, 1993) and the productions of ejaculates (Dewsbury, 1982; Galvani and Johnstone, 1998). For this behavior to be adaptive, these individuals are expected to benefit one way or another.

In general, mate choice is less common in males, being reported in only 58 insect species, distributed among 11 orders and 37 families (Bonduriansky, 2001). There is now a growing number of observations of male choice which is seen in a wide range of taxa including insects (Bonduriansky, 2001; Byrne and Rice, 2006), birds (Jones and Hunter, 1993), and fishes (Amundsen and Forsgren, 2001). These studies suggest that male mate choice is predicted to be adaptive when variance in female fitness is large and males experience a cost to mating such that they cannot inseminate all females encountered (Burley, 1977; Parker, 1983; Owens and Thompson, 1994; Johnstone *et al*., 1996; Kokko and Monaghan, 2001). However, the empirical evidence is limited.

The most obvious character influencing the reproductive value of the female is her fecundity (Bonduriansky, 2001). When mating opportunities are constrained, males that show a preference for more fecund females will benefit directly by increasing the number of offspring they produce (Katvala and Kaitala, 2001). However, models of the evolution of male choice suggest that male choice will tend to breakdown when males target arbitrary female traits rather than those that reliably signal fecundity (Kokko and Johnstone, 2002; Chenoweth *et al*., 2006; Servedio and Lande, 2006). Therefore, male preference for female traits may be an indirect way of assessing female fecundity. The characters used by the males to select the females are generally virginity, her size, age, and gravid status (Bonduriansky, 2001). Thus, there is a need to understand how male choice is related to such traits.

D. ananassae is one of the species that belongs to the genus *Drosophila* and has been employed in the present investigation. 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 1985a, b). Absence of male crossing over, high level of inversion polymorphism, and high mutability are the features which make it useful for certain genetic studies. Female age influence on reproduction and male mating success has not been studied. Therefore, monomorphic and polymorphic strains of *D. ananassae* have been employed in the present investigation to study relationship of female age, reproductive success, and inversion system.

Materials and Methods

Experimental stocks of monomorphic and polymorphic strains of *D. ananassae* were established from isofemale lines of *D. ananassae* obtained from out-bred populations collected at semi domestic localities in Mysore, Karnataka, India (Prathibha and Krishna, 2010). These isofemale lines were maintained at 21±1ºC and relative humidity of 70%. When larvae appeared, eight third instar larvae from each isofemale line were used to analyze presence or absence of inversions. This procedure was continued for 3 generations to establish monomorphic (inversion free) and polymorphic (with inversion) strains and to allow flies to acclimatize in the laboratory. In the 4th generation 5-6 day old flies were used to collect synchronized eggs (± 30 min) using Delcour's procedure (1969). Eggs (100) were seeded in a vial containing wheat cream agar medium. When adults emerged, virgin females and unmated males were isolated within 3 hr of their eclosion and were aspirated into a new vial containing wheat cream agar medium. These flies were aged as required for the experiment. Young aged females (2-3 day old), middle aged females (17-18 days old), and old aged females (32-33 days). These females were kept individually in culture vials containing wheat cream agar medium and were transferred to a new vial containing wheat cream agar medium once in a week until they were used in the experiment. Male flies were aged in the same environment for 5-6 days.

Female age influence on mating success in monomorphic and polymorphic strains

Young, middle, old aged females and 5-6 day old bachelor males of monomorphic and polymorphic strains of *D. ananassae* were used to study whether or not inversion system influences male mating preference for female age. Two females (young, middle/young, old/middle, old) and 5-6 day old male were aspirated into an Elens-Wattiaux (1964) mating chamber. Indian ink was painted to one of the females on the thorax. (The effect of paint was tested before commencing the experiment by painting young female in one trial and middle/old aged female in an alternate trial and allowing them to mate. In 27 out of 50 trials, middle aged females were mated, and in the remaining 23 out of 50 trials old aged females were mated ($\chi^2 = 0.32$; df = 1; $p > 0.05$). Results showed insignificant difference suggesting that painting did not have influence on the performance of the flies). Each pair was observed for 1 hr. When mating occurred, pairs in copulation was aspirated out from the mating chamber and aspirated into a new vial containing wheat cream agar medium. A total of 50 trials were made for each combination and Chi-square analysis was carried out to the male mate choice data. Separate experiments were made for monomorphic and polymorphic strains.

Female age influence on wing length in monomorphic and polymorphic strains

Virgin young/middle/old aged females were individually sacrificed to count female wing length following the procedure of Krishna and Hegde (1997). From the same female, wing length was also measured using 100× following the procedure of Hegde and Krishna (1997). A total of 50 trials were made separately for each of the three female age classes.

Female age influence on mating activities in monomorphic and polymorphic strains

To study relation between female age related changes in mating activities, fecundity, fertility, and inversion system, a male (5-6 days old) along with a female (young/ middle/ old) were aspirated into an Elens-Wattiaux (1964) mating chamber and observation was made for 1 hr. Mating latency (time between introduction of male and female together into a mating chamber until initiation of copulation of each pair) and copulation duration (time between initiation of copulation to termination of copulation of each pair) were recorded. We also quantified courtship acts such as tapping, scissoring, vibration, licking, circling, ignoring, extruding, and decamping following the procedure of Hegde and Krishna (1997).

Separate experiments were carried out for monomorphic and polymorphic strains. Two-way ANOVA followed by Tukey's Honest Post hoc test were carried out on mating latency, courtship activities, copulation duration data using SPSS 10.1 software.

Results

In both monomorphic and polymorphic strains of *D. ananassae* males generally chose to mate with middle aged females more frequently than young or old aged females. Middle aged female success in crosses involving young and middle aged females was 31 ($\chi^2 = 1.40$, df = 1; $P > 0.05$; N = 50) in monomorphic strains and 35 ($\chi^2 = 0.4$, df = 1; $P > 0.05$; N = 50) in polymorphic strains. Middle aged female success in crosses involving old and middle aged females was 35 ($\chi^2 = 0.4$, df = 1; $P > 0.05$; N = 50) in monomorphic strains and 36 ($\chi^2 = 0.45$, df = 1; $P > 0.05$; N = 50) in polymorphic strains. Young aged female success in crosses involving young and old aged females was 32 ($\chi^2 = 0.28$, df = 1; $P > 0.05$; N = 50) in monomorphic strains and 34 ($\chi^2 = 0.36$, df = 1; $P > 0.05$; N = 50) in polymorphic strains.

Table 1. Mean wing length of mated female of monomorphic and polymorphic strains in male choice experiment of *D. ananassae*.

Male	Strains	Females in male Choice experiment	Number of females mated	Wing length (in mm)	t-value
5-6 days male	Mono	YAF OAF	32 18	1.97 ± .02 1.99 ± .02	0.28^{NS}
	Poly	YAF OAF	34 16	2.00 ± .02 2.10 ± .03	2.12*
	Mono	YAF MAF	19 31	1.98 ± .03 1.99 ± .02	0.19 ^{NS}
	Poly	YAF MAF	15 35	2.05 ± .04 2.07 ± .02	0.32 ^{NS}
	Mono	MAF OAF	35 15	1.99 ± .02 1.98 ± .03	0.27 ^{NS}
	Poly	MAF OAF	36 14	2.08 ± .02 2.08 ± .04	0.12 ^{NS}

*P< 0.005; NS – insignificant

Note: 1. YAF- Young age female; OAF- Old age female; MAF- Middle age female.
2. Mono- Monomorphic strain, Poly- Polymorphic strain.

Polymorphic strains had greater mean wing length of Table 1 revealed that in both monomorphic and polymorphic strains insignificant variation was observed in mean wing length of mated female among female age classes (Young, middle, and old), between strains (monomorphic and polymorphic) and also interaction between female age and strains (young, middle, old and monomorphic, polymorphic).

Mean courtship, mating activities of females of different age classes mated to males in monomorphic and polymorphic strains are provided in Table 2. It was noticed that, in both monomorphic and polymorphic strains, males mated with middle aged female had taken shortest time for mating initiation, copulated longest, performed greatest courtship activities, *i.e.*, tapping, scissoring, vibration, licking, circling. While males mated with old aged female had taken longest time for initiation of mating, copulated shortest, and showed least courtship activities, middle aged females showed least rejection responses to courting male. Old aged females show highest rejection responses to courting males. Male and female courtship activities in polymorphic strain, although not showing significant variation in all the activities studied, had greater activities compared to monomorphic strains. Two way ANOVA followed by Tukey's Honest Post hoc test (Tukey's test) carried out on courtship, mating activities data showed significant variation between strains and between female age classes, however insignificant difference in the interaction between strains and female age classes except licking and ignoring. Tukey's test showed middle aged females took significantly shorter time for mating initiation, males performed greatest courtship activities, copulated longest, and middle aged females had significantly greater compared to young or old aged female. Similarly males performed significantly greater courtship activities to young aged females and copulated longest than old aged female.

Discussion

In *Drosophila* high cost of reproduction is due to cost arising from factors such as energetically expensive courtship displays, the production of ejaculates, and time loss during displaying different courtship (Bonduriansky, 2001). In both monomorphic and polymorphic strains, males of *D. ananassae* prefer to mate with middle aged females more frequently over young or old aged females. This suggests that in *D. ananassae* female age is an important determinant of male mate choice. In other words males of *D ananassae* do not show the same levels of interest in females of different age classes she encountered. This supports the suggestion of Gowaty *et al*. (2003) who, while working on *D. melanogaster*, have also pointed out that males of *Drosophila* do not show the same level of interest in all the females he encountered and provided evidence that males have also evolved to mate selectively. Our study also confirms the earlier studies of existence of male mate choice for females in other insects, too (Bonduriansky, 2001). Thus these studies in *Drosophila* and other insects suggest that male preference for female traits may be an indirect way of assessing female fitness.

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

		Female age (in days)			F-values		
Parameters	Strains	Young (2-3 days)	Middle (17-18 days)	Old (32-33 days)	F-1 = between strains (df-1, 294)	F-2 = between ages (df-2, 294)	F-3 = between strains & ages (df-6, 294)
Mating latency	Mono	24.36 ± .77^{b}	14.48 ± .48^{a}	32.66 ± .82^{c}	53.14**	300.96**	.27 ^{NS}
	Poly	19.64 ± .58^{b}	10.78 ± .26^{a}	28.14 ± 1.10^{c}			
Tapping	Mono	8.44 ± .19^{b}	10.36 ± .27^{c}	6.96 ± .21^{a}	63.54**	90.83**	.86 ^{NS}
	Poly	9.92 ± .23^{b}	12.54 ± .40^{c}	8.64 ± .27^{a}			
Scissoring	Mono	9.54 ± .31^{b}	11.12 ± .35^{c}	7.86 ± .18^{a}	36.69**	62.73**	.75 ^{NS}
	Poly	10.88 ± .41^{b}	13.16 ± .29^{c}	9.24 ± .32^{a}			
Vibration	Mono	10.22 ± .26^{b}	12.78 ± .37^{c}	7.58 ± .22^{a}	35.36**	114.38**	.53^{NS}
	Poly	11.62 ± .34^{b}	14.14 ± .40	9.54 ± .29^{a}			
Circling	Mono	4.12 ± .10^{b}	5.16 ± .17^{c}	3.18 ± .16^{a}	4.92*	80.12**	1.04^{NS}
	Poly	4.26 ± .13^{b}	5.76 ± .25^{c}	3.38 ± .15^{a}			
Licking	Mono	3.86 ± .19^{b}	4.46 ± .18^{c}	2.88 ± .13^{a}	32.08**	67.39**	5.61*
	Poly	4.68 ± .22^{b}	6.02 ± .26^{c}	3.16 ± .10^{a}			
Ignoring	Mono	4.52 ± .14^{b}	3.24 ± .17^{a}	7.68 ± .17^{c}	42.04**	354.59**	3.18*
	Poly	4.12 ± .20^{b}	2.14 ± .09^{a}	6.52 ± .18^{c}			
Extruding	Mono	4.24 ± .10^{b}	2.70 ± .12^{a}	5.94 ± .25^{c}	16.53**	111.42**	.78^{NS}
	Poly	3.42 ± .20^{b}	2.32 ± .17^{a}	5.12 ± .28^{c}			
Decamping	Mono	3.22 ± .13^{b}	2.38 ± .07^{a}	4.94 ± .23^{c}	5.65*	74.92**	.96^{NS}
	Poly	2.98 ± .22^{b}	2.18 ± .14^{a}	4.26 ± .26^{c}			
Copulation duration	Mono	3.96 ± 0.04^{b}	4.13 ± .01^{c}	3.44 ± 0.03^{a}	20.88**	187.71**	.95^{NS}
	Poly	4.08 ± 0.04^{b}	4.34 ± .03^{c}	3.55 ± 0.04^{a}			

*P< 0.005; **P< 0.001; NS – insignificant

Note: 1) Different letter 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. 3) Mono- Monomorphic strain, Poly- Polymorphic strain.

Like female mate choice even in male mate choice too, it was difficult to separate between male choice and female-female competition and differences in female motivation to mate (Byrne and Rice, 2006). Therefore, we can hypothesize that in *D. ananassae* middle aged females are more eager to mate than young or old age females. This agrees with earlier studies of sexual selection in different species of *Drosophila* too (Speith, 1952; Manning, 1961; Hegde and Krishna, 1997; Byrne and Rice, 2006; Prathibha and Krishna, 2010).

Females of young, middle, and old age of *D. ananassae* used in our study were virgins and reared in same condition throughout their experiment suggesting that the observed greater mating success of middle aged females may not be due to difference in the life history and rearing condition. Instead it could be the result of age specific reproductive success in females.

Studies in insects have also found a positive correlation between female size and measure of wing length (Branquart and Hemptinne, 2000). Even in *Drosophila* studies of Robertson (1957) have found positive correlation between female sizes. In the present study we sacrificed the flies which were used for measuring wing length to understand the relationship between female ages wing length. It was found that there was an insignificant difference in mean female wing length among females of different age classes in monomorphic as well as polymorphic strains (Table 1). This suggests that female age has no influence on female body size.

In *Drosophila* successful mating depends of male activity and female receptivity (Manning, 1961; Spieth, 1968). Table 2 shows in both monomorphic and polymorphic strains of *D. ananassae* middle aged females mated faster, copulated longer than young or old aged females. This suggests that middle age females were more receptive than young or old aged females. This supports earlier studies of *Drosophila* suggesting that females which mate faster and longer are more receptive than the females which mate slower and copulate shorter. This is because mating latency (time taken for initiation of mating) and copulation duration (time between initiation of copulation to termination of each pair) are good estimates of female receptivity (Spieth and Ringo, 1981; Hegde and Krishna, 1997).

In turn males of *D. ananassae* showed greater courtship activities to middle aged females compared to young or old aged females suggesting influence of female age on male courtship activities in too (Table 2). Through these courtship activities males of *D. ananassae* not only convey chemical, auditory, visual signals to middle aged females better and try to convince the middle aged female faster for mating than young or old aged females. This agrees with earlier studies of *Drosophila* that males which perform greater courtship activities are better mates and obtained greater mating success than those males which do not show high level of courtship activities (Hegde and Krishna, 1997).

Thus these studies suggest that males of *D. ananassae* exercised mate choice to obtain direct fecundity benefits, and we also found occurrence of age specific reproductive success in females of *D. ananassae* which is independent from influence of inversion system.

Acknowledgment: The authors are grateful to the Department of Studies in Zoology and Principal, Yuvaraja's College, University of Mysore, for providing facilities.

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Genetic evidence for differential activities of $G\alpha_O$ isoforms in *Drosophila melanogaster*.

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$G\alpha_o 47A$ encodes two isoforms of the $G\alpha_O$ subunit ($G\alpha_O 1$ and $G\alpha_O 2$) in *Drosophila melanogaster* (de Sousa *et al.*, 1989; Schmidt *et al.*, 1989; Thambi *et al.*, 1989; Yoon *et al.*, 1989). These two isoforms are